Science Progress.

No. 26. April, 1896. Vol. V.

THE GENERAL BEARINGS OF MAGNETIC OBSERVATIONS.

IF necessity be the surest prompter of invention, it is not too much to say that the necessity of the navigator has been a most potent factor in producing the observer of the elements of Terrestrial Magnetism. The traveller on land might rest during darkness until daylight enabled him to resume his journey; but the seaman on the trackless ocean was dependent upon the indications of his compass by day and night; and after the discovery of Columbus that the magnetic Declination or Variation of the needle from the direction of the geographical North varied in amount with the Latitude and Longitude, a new impetus was given to observation.

The publication of Gilbert's grand discovery that the earth is a magnet and the director of the freely suspended needle, followed by the discovery of the secular change in the value of the Declination, naturally added to the desire of both landsmen and seamen to know as much as possible concerning that great magnet, both from purely scientific reasons and to meet the practical ends of the navigator. Thus the seventeenth and eighteenth centuries were remarkable for the number of observers both of the magnetic Dip and Declination.

So important had a correct knowledge of the Declination become to the requirements of navigation, as early as the close of the seventeenth century, that Halley, under the

immediate auspices of the Government, made his celebrated voyage over the Atlantic Oceans in a man-of-war, in order that intelligent observation should set at rest much that was doubtful. The results of this voyage, combined with the observations of previous navigators, were embodied in his celebrated chart of lines of equal value of magnetic Variation or Declination, the first of its kind and of so convenient a form that charts of equal values of the three magnetic elements are to this day the most acceptable form for representing the combined results of magnetic observations made over large areas of sea and land, as well as of the special magnetic surveys which in recent years have been made in various countries.

Here we may pause to consider the word Declination as applied to the angle which the direction of the horizontal magnetic needle makes with the true meridian. Many magneticians object to the word, but no better has yet been proposed or at any rate accepted; the result being that while observers on land use the term, seamen adhere firmly to the expression "Variation of the Compass". This is as might be expected when it is remembered that navigators look upon the word Declination as connected with the position of the sun and other heavenly bodies, and would find it most inconvenient to have the same word in daily use, meaning two totally different things.

During the eighteenth century charts of the magnetic Declination were published by Mountaine and Dodson, Bellin, and Churchman, and for their time may be considered as fair approximations to the truth. Churchman's design was not only to give values of the Declination but to furnish the seaman with a means of ascertaining the Longitude, an ambitious project, especially as we now know there were probably considerable elements of error in these charts caused by local magnetic disturbance of the observing compass on land, and from the iron used in construction disturbing the compass on board the ships.

This latter source of error was only beginning to be viewed in its true light at the close of the eighteenth century.

In the years 1801-2 Commander Flinders of H.M.S. *Investigator*, then surveying the southern coasts of Australia, found that when his vessel's head was north or south by compass the observed Declination agreed very nearly, but when she lay with her head east or west, it differed largely. Moreover these errors on the east and west points of the compass had the opposite sign to those observed in England.

Flinders, however, had supplemented the existing scanty knowledge of the distribution of the Dip over navigable waters by several observations of his own in northern and southern latitudes, and from these he drew the conclusion that the errors in the Declination observed on board ship were caused by magnetism induced by the earth in the vertical iron of the ship, and changed in value proportionally to change of Dip. Here Flinders was wrong, as the errors were really proportional to the tangent of the Dip.

In spite of this mistake he was enabled from his knowledge of the Dip to conceive the idea of so placing vertical bars of iron that they produced an equal and opposite effect on the compass to that of the ship in all latitudes, and thus invented what is now called the Flinders bar, one of the most important correctors of compass disturbance in the iron and steel ships of the present day.

In 1814 Flinders induced the Admiralty to have experiments made on board men-of-war at Portsmouth, Sheerness, and Devonport, to ascertain the amount of the magnetic disturbance of the compass caused by the iron in each ship. The chief reason for making these experiments was to show the necessity for ascertaining and applying these errors to ensure the safe navigation of the ships, but it had also a direct bearing in enabling observers to eliminate the hitherto inexplicable divergencies in the values of the Declination observed in different ships in the same geographical position. The results of these experiments bore no immediate fruit, for with the death of Flinders the subject was temporarily neglected.

In 1819, Hansteen published his *Magnetismus der Erde*

with an atlas containing charts of the elements Declination and Dip for different epochs between the years 1600 and 1787. These charts were in a large measure compiled from observations made with imperfect instruments and subject to the causes of error already mentioned attending both land and sea results. Hansteen, however, considered them of sufficient value to enable him to draw certain important conclusions with regard to the cause of the secular change of the magnetic elements. Thus he not only concurred with Halley that the earth considered as a magnet had four poles or points of attraction, but computed their geographical positions. Further than this, he computed that to account for the secular change these four supposed poles revolved round the terrestrial poles, each pole occupying a widely different number of years to complete the revolution.

If these theoretical results had been true, a great advance would have been made not only in the science of terrestrial magnetism but in its practical bearing on the requirements of the present day.

Although Humboldt had about the year 1800 shown that the intensity of the earth's magnetism varied with the latitude, the general distribution of that magnetic element was so little known that we may with our present extended knowledge consider that Hansteen's conclusions were based on insufficient data. In fact the idea of the earth being a magnet with four poles has long since been abandoned in favour of there being one pole with two foci of intensity in each hemisphere, and reasons will be given further on which tend to throw doubt on there being any revolution of these two magnetic poles round their adjacent terrestrial poles.

Subsequently to Hansteen's charts there appeared those of the Declination by Yeates, Duperrey, and by Barlow in 1836. These were useful to navigation but helped very little towards the solution of the problem of the ever variable distribution of the earth's magnetism.

Besides this by the year 1835 the iron-built ship had appeared on the ocean and a correct knowledge of the

three magnetic elements became a necessity in solving the problems which the magnetism of different iron ships presented.

With Gauss's invention of the absolute horizontal force magnetometer in 1833, many hitherto unknown movements of the magnetic needle of the highest interest were discovered, which with the coarser instruments previously in use lay concealed. This discovery gave the desired impetus to the scientific men of that epoch, and the period included in the years 1835-45 was "a time of unparalleled activity in the extension of systematic and accurate magnetical observations over the earth's surface".

Whilst most of the continental nations joined in this movement, the principal share in the work was divided between Germany, Russia, and England in Europe, and the United States in America. But before the splendid series of simultaneous observations made on the continent, and four British colonial observatories were organised, Gauss in 1839 published his general theory of Terrestrial Magnetism coupled with a series of charts of the three magnetic elements for the whole world, based upon observations made at ninety-two selected stations distributed over the earth's surface; and it may be remarked that Gauss's charts not only gave results in fair accordance with observation in explored regions, but also as afterwards proved in Antarctic latitudes hitherto unvisited by man.

The proof came in the years 1839-43, when Ross's Antarctic voyage of exploration was carried out in the interests of terrestrial magnetism. Besides the importance of a knowledge of the general distribution of the magnetic elements in those regions, one great aim of this expedition was to reach the south magnetic pole. This was found to be impossible, but sufficient data were collected to give its approximate position. Whilst this Antarctic magnetic survey was being completed, that of British North America was also undertaken with the result of the determination of the locality of one of the foci of greatest intensity in the northern hemisphere.

The results of these surveys formed, as will be well

remembered, a valuable series of "contributions" to terrestrial magnetism by Sabine, and, coupled with every available observation between the years 1818 to 1876, formed the materials for the series of charts entitled "The Magnetic Survey of the Globe" for the epoch 1842·5. Each map gave normal lines of equal values of the Declination, Inclination and Intensity. Although it may be said that from the Arctic circle to the Antarctic, the direction of the lines was efficiently given by observation, the lines within those circles were largely taken from Gauss's computed lines modified to agree with observation.

Another difficulty in compiling these charts of Sabine's with accuracy lay in the uncertain knowledge of the secular change then available, and which had to be applied to observations made so far apart in time.

Sabine's charts are doubtless the best we have for the epoch 1842·5, but in the light of the requirements of modern science they leave much to be desired as regards the Antarctic regions. The observations south of 60° S. were made entirely on board ships, where the errors of the compass sometimes exceeded 50° due to the horizontal forces in the ship, thus rendering accurate observations of the Declination very uncertain and correction of the observed Inclination very difficult; besides which there are no records of the ship's disturbing force in the vertical direction.

Naval requirements, however, did not permit of any delay in publishing magnetic charts affecting navigation, for in 1846 the Hydrographer of the Admiralty requested Sabine to provide charts of the Declination for the Atlantic Oceans from 60° N. to 60° S. These were largely used until Evans's chart of the Declination for the whole navigable world was issued in 1858.

The excellent work of Flinders already referred to, of ascertaining from his knowledge of terrestrial magnetism the chief cause of the deviation of the compass in wood-built ships, and providing a corrector for those deviations, had to be followed up on a much larger scale and with more exact methods in the iron-built ship, which, in that

period of activity in terrestrial magnetic science—1835-45—was rapidly increasing in numbers on the ocean.

Thus in 1835 observations were made on board iron ships showing that they acted as a magnet on their compasses, but there was nothing to show in the results what the causes of this condition of the iron ship were, until Poisson in 1838 published his celebrated "Memoir on the deviations of the compass produced by the iron in a ship". This was a rigorous mathematical investigation of the subject, showing that the deviations of the compass were due to induction in the ship by the magnetic force of the earth.

If the iron ship had simply been built for service in one locality, a limited knowledge of terrestrial magnetism would have sufficed to elucidate the causes of her magnetic condition; but she was destined to traverse every navigable sea over large changes of magnetic latitude, hence the necessity for an accurate knowledge of the distribution of magnetism over the great parent magnet, in order to determine the magnetic condition of her comparatively minute offspring the magnetised iron ship; and this at all times and in all places in the interests of navigation. Observations of the terrestrial magnetic elements were therefore an absolute necessity if iron-built ships were to be substituted for those of wood.

The ability to predict the deviation of the compass on change of latitude did not, however, satisfy Airy, for after a remarkable mathematical investigation of iron ship's magnetism of a less rigorous character than Poisson's, but sufficiently accurate for his purpose, he in 1839 proposed his methods of annulling the deviation of a ship's compass by means of magnets and soft iron, so arranged as to produce equal and opposite magnetic effects to that of the ship. Provided with Airy's admirable and simple directions this method of correction was comparatively easy in one latitude, but experience at sea, especially in voyages to the Cape of Good Hope, showed that every iron ship required a different application of Airy's correctors.

To discriminate between the amount that was to be

corrected by permanent magnets, by horizontal soft iron, and by vertical soft iron, an accurate knowledge of the magnetic elements Dip and Intensity obtained from observations on land and at sea was essential.

Before dismissing the subject of the above application of magnetic observations, it may be remarked that we have now heavily armed, protected steel cruisers steaming over all parts of the world with less change of deviation of the compass than the wood-built *Erebus* and *Terror* of Ross's Antarctic expedition, and this remarkable result could not have been achieved if the terrestrial magnetic observer had not done his work.

Moreover, if magnetic observations are not continued the secular change of the magnetic elements will soon commence to mar the precision with which our rapidly moving ships traverse the globe.

The voyage of the *Challenger* in 1872-76 contributed the most valuable series of observations of the magnetic elements in modern times, when the large areas of the principal oceans traversed by that vessel during three and a half years are taken into consideration. These observations, combined with those taken from every available source, both British and foreign, between the years 1865-87, formed the materials from which the magnetic charts of 1880 were compiled (see vol. ii., *Physics and Chemistry*, part vi., *Voyage of H.M.S. "Challenger"*).

The *Challenger* only crossed the Antarctic circle at one point in longitude 78° E., and, therefore, although we know large secular changes to be going on south of 40° S. we have no measure of the amount, nor anything like an accurate knowledge of distribution of the earth's magnetism in those regions. This points to the necessity for a new Antarctic expedition.

In the year 1888 the late Professor J. C. Adams was provided with a complete set of magnetic charts for the two epochs 1842·5 and 1880 previously mentioned, and as it was known he had directed his profound mathematical ability to the analysis of the results contained in them, it was hoped that some new and important light might be

thrown upon the bare facts presented. His lamented death occurred without his publishing any results.

If, however, reference be made to the report on the magnetical results of the *Challenger*, a discussion of the secular change is contributed founded in a great measure on a comparison of those charts. The outcome of this discussion is to throw considerable doubt upon the theory that the motion of the magnetic poles round the terrestrial is the cause of secular change; in fact, that the magnetic poles remain fast, and we must look elsewhere for the cause whatever it may be.

Magnetic observations have so far been considered in their all-important bearing as necessary to safe navigation in wood-built ships, and in a far higher sense as indispensable to that of the iron- or steel-built ships which now cover the ocean; the magnetic charts hitherto generally required for these purposes being those on which normal lines of equal values have been given, but something more is now needed.

Observation in comparatively recent years has shown that not only are there large "regional" magnetic disturbances extending over large areas of land, but that in moderate depths of water where the largest ship can navigate freely, the land below is also found to have considerable areas of local magnetic disturbance which, if not allowed for, may in thick or foggy weather lead ships into danger by seriously disturbing their compasses.

The United States have done excellent work in producing charts of iso-magnetic lines, or charts in which the chief local magnetic disturbances are recognised, and the full results of observation recorded. The magnetic surveys of Rücker and Thorpe in the British Isles, of Moureau in France, of Rijckevorsel in Holland and elsewhere, have thrown considerable light on the magnetic conditions of those countries, but there remain whole continents to be covered by the observer.

The direction of the iso-magnetics too from the deep sea to the dry land of the coasts is an extension of the subject, which the observer has hardly touched as yet, but

one affecting the safety of navigation, as well as the question that has been raised, whether the water areas of the globe are as a whole more, or less magnetised than the land areas.

To possess charts of iso-magnetic lines for even a few countries is an evidence of considerable advance in the knowledge of terrestrial magnetism, for if reference be made to Sabine's lines of intensity in his contribution on the magnetic survey of North-West America it will be found that he rejected certain observations he considered abnormal and defective, which Lefroy the observer considered to be his best and naturally retained in his map; the result being a considerable difference in the form of the curves adopted by the two magneticians, Sabine giving normal curves, Lefroy iso-magnetics.

Respecting the local disturbances of the needle which have been so clearly proved, the question naturally arises, whence the cause of these disturbances? It is now believed by many, if not finally accepted, that Rücker and Thorpe have answered the question by the results of their laborious survey of the British Isles, coupled with Rücker's elegant investigations as to the permeability of specimens of the rocks taken from the localities in which magnetic disturbances were found. Their answer is to the effect that these disturbances, which have been found to extend over a region 230 miles long by about 110 miles broad, are due to induction by the earth's magnetism in rocks of different permeability, either present as in the basalts on the surface or concealed by superficial deposits.

These results are distinct from the extraordinary disturbances of the needle when in the immediate vicinity of permanently magnetised rocks, and when the radius of disturbance may be only as many feet as the extent of the regional disturbance is in miles.

The points of interest in the question of regional magnetic disturbance are not confined to the magnetician, for the geologist cannot afford to neglect the valuable information the magnetic needle affords. Thus although Rücker and Thorpe have since made a second and more elaborate survey of the British Isles, their remark of 1890

that "the kingdom can be divided into magnetic districts in which the relations between the direction of the disturbing forces and the main geological characteristics are so suggestive as to be worthy of careful statement and further investigation," not only holds good, but has received confirmation.

The mining engineer is deeply interested in a knowledge of the Declination. Charts of normal lines are of great use to him whether above or below the earth's surface, but especially below when he has no other guide. To such an one a knowledge of regional magnetic disturbance as deduced from surface observations is most important, as it tells him that he is in the neighbourhood of magnetic rocks, the disturbing effect of which on his compass needle may be far greater in the depths of his mine and turning it into a treacherous guide.

We have now considered magnetic observations in a measure from the point of view of the immediate practical results which their scientific treatment produces, but who will say in this great maritime nation that the work of magnetic observers, even if solely to make navigation possible, is not worthy of the fullest consideration?

There is besides a vast field of inquiry for the observer of terrestrial magnetism in unravelling the secrets of the earth considered as a magnet, and the ceaseless change of its magnetic condition which the needle tells us of, for which no immediate practical result can be foreseen, yet is worthy of the attention of the ablest physicists and most advanced mathematicians.

Inquiry into the causes of the secular change is one requiring the fullest attention, but observation has not yet done sufficient work. It certainly has done much in certain countries, and for a large portion of the world as regards secular change in the past, and data obtained for predicting future changes for a few years, but only one expedition has examined the Antarctic regions magnetically, and it is doubtful if any substantial progress will be made until a second expedition is made thither, one profiting by the experience of its precursor, and equipped with possibilities for work hardly hoped for by Ross.

It may be remarked in passing that a remarkable alteration in the amount of the secular change has been noticed in the Declination and Inclination at the following observatories: Bombay, Batavia, and Hong Kong about the period of the eruption of Krakatoa in 1883. This may be only a coincidence, but may it not also point to the possibility that the changes below the surface of the earth which culminated in that mighty explosion, and may still be at work, have had, and continue to have, magnetic effects which are recorded by the needles at those observatories?

Critical investigations have for many years been directed to the elucidation of the causes of the observed diurnal variations of terrestrial magnetism. This work was long seriously retarded by the various methods adopted at different observatories for recording their results, obliging those who entered upon a comparison of such results to go through a tedious conversion of them into a common method. It may be said that the first large departure from this objectionable practice occurred when the International Polar Inquiry of 1882-83 was undertaken by the various expeditions.

This was an important step in the right direction, but there remains much to be done, as shown by the ten reports of the British Association Committee on "the best means of comparing and reducing magnetic observations". Their last report consists of an able and suggestive paper by Dr. Chree, being the analysis of the results of five years' observations on "quiet days" at Kew, and is well worthy of attention as indicative of the present state of our knowledge as regards the diurnal variation of the three magnetic elements.

Such investigations only encourage one in the hope that the much required observations in southern latitudes may be undertaken. The observatories at the Cape and Melbourne could do invaluable work if it were carried out on the lines of Kew, for example.

Lastly, what more is there to be said about magnetic observations and their bearings? We do not know why the earth is a magnet, the cause of the secular change of its

magnetism, why it is subject to solar diurnal, lunar diurnal, sidereal diurnal and the other variations and disturbances, nor the cause of magnetic storms, although we can observe connections between them, earth currents, and auroræ. Whether the causes of all these exist below the surface of, or are external to, the earth, or are a combination of the two, has still to be learnt, and it seems hardly too much to hope that the restless needle will sooner or later be the means of opening up sources of knowledge invaluable to cosmical science, as well as to those only concerned with the planet upon which they dwell.

When the causes of the secular change are understood there will be no difficulty in providing the navigator with magnetic charts for years in advance, much as the tides can now be tabulated for his use. In the latter case observation has done its work for several frequented ports, in the former case a vast amount remains to be done, and the word that goes forth is still, as Lord Kelvin thrice said on a kindred subject connected with ships' magnetism, "Observe".

ETTRICK W. CREAK.

THE PRESENT POSITION OF THE CELL-THEORY.

PART I.

A FEW years ago a discussion of the cell-theory would have seemed superfluous. To-day, partly because of criticisms which have been directed against the theory, partly because of the great increase of our knowledge respecting cell-structure, the advantage and even the necessity of such a discussion will be admitted by everybody who has read and reflected on the subject. In what follows, I propose to examine the cell-theory in the light of recent criticisms and researches. I set out with the intention of avoiding anything in the shape of polemical writing, but I fear that I have in places fallen away considerably from the course which I had proposed. In a much disputed subject controversy is inevitable, a circumstance which need not be regretted, for controversy is the whetstone of argument, and obliges those who engage in it to be doubly careful both of their facts and of the language in which they express them. My antagonists will, I hope, give me the credit of the desire to deal fairly with their arguments and criticisms, and will acquit me of unnecessary bitterness. It has been my object to elucidate the subject in hand rather than to try to gain a dialectical advantage.

It is advisable, before entering on the examination, to have a clear conception of what the cell-theory really is. This is the more necessary because one of its most recent critics, Mr. Adam Sedgwick, has complained than nobody will define the theory in an exact manner; it is, he says, a kind of phantom which takes different forms in different men's eyes. I have shown in another place that this statement is hardly fair, because there are some authors whose researches on cytology entitle them to speak with authority who have recently defined the cell-theory in a very precise manner, though it may be conceded that there are biologists

whose views are not so exact, and who habitually commit themselves to statements which on careful examination may prove to be altogether untenable.

It was pointed out some time since by Whitman,[1] and I have since emphasised the fact,[2] that in his broad generalisations Schwann defined the cell-theory in a very exact manner, and that the words originally used by him are perfectly applicable to the cell-theory as it has been held up to the present time. In saying this, I do not forget that Schwann held some very erroneous views as to the nature and structure of cells, which he regarded as vesicles, filled with fluid, which made their appearance in a structureless matrix, named for this reason, a cytoblastema. But Schwann's work consisted of two parts, a statement of observations, which have proved to be entirely erroneous, and a theory of organisation, which has been very fruitful of results. He was careful to say that his theory was only a provisional explanation which suited the facts as nearly as possible, and it is a great merit of the theory that it afforded such an insight into organisation that the essential part of it did not cease to be serviceable long after the "facts" on which it was founded were shown to be, for the most part, false. We need not therefore concern ourselves with the fact that Schwann's conceptions of the origin and structure of cells were false, but we may examine his theory and see how much of it we may hold to, and how much we must reject at the present day.[3]

Schwann was a very cautious writer, and the quotations which are given below will dispose effectually of the state-

[1] C. O. Whitman, "On the Inadequacy of the Cell-theory of Development," *Journal of Morphology*, viii., p. 639, 1893.

[2] G. C. Bourne, "A Criticism of the Cell-theory," *Quart. Jour. Microscopical Science*, xxxviii., p. 137, 1895.

[3] A large part of Schwann's theory of cells, *viz.*, that part of it which compared cell-formation to the process of crystallisation, was soon shown to be untenable. But as this part was based on his erroneous views on the structure and origin of cells, I have passed it over, since the falsity of his views on this subject involved the falsity of as much of his theory as was founded on them.

ment which stands in the first paragraph of Whitman's work, that he believed that in cell-formation *lies the whole secret of organic development.* There are, says Schwann, two possible theories on the subject of organic development: (1) The organism theory, namely, that there is an inherent power modelling the body in accordance with a predominant idea. (2) The physical theory, namely, that the fundamental powers of organised bodies agree essentially with those of inorganic nature. Rejecting the former of these two theories as being outside the domain of physical science, Schwann went on to write:[1] "We set out with the supposition that an organised body is not produced by a fundamental power which is guided in its operation by a definite idea, but is developed according to the blind laws of necessity by powers which, like those of inorganic nature, are established by the very existence of matter. As the elementary materials of organic nature are not different from those of the inorganic kingdom, the source of the organic phenomena can only reside in another combination of these materials, whether it be in a peculiar mode of union of the elementary atoms to form atoms of the second order, or in the arrangement of these conglomerate molecules when forming either the separate morphological elementary parts of organisms, or the entire organism. We have here to do with the latter question solely, whether the cause of organic phenomena lies in the whole organism or in its separate elementary parts. If this question can be answered a further inquiry still remains as to whether the organism or its separate elementary parts possess this power through the peculiar mode of combination of the conglomerate molecules or through the mode in which the elementary atoms are united into conglomerate molecules."

Is it not perfectly clear from this that Schwann fully recognised that there was a further question underlying

[1] Th. Schwann, *Microscopical Researches into the Accordance in the Structure and Growth of Animals and Plants.* Translated by Henry Smith. London: Printed for the Sydenham Society, 1847.

the cell-theory, and do not the words which he used with regard to the union of elementary atoms to form atoms of the second order show a prescience of the assumptions which would have to be made to explain the powers manifested by cells? Because he confined himself to the one question, it is not fair to say that Schwann had not a clear appreciation of the importance of the other. I may relate, in this connection, an anecdote which will finally clear Schwann's reputation from the reproach fastened upon it. Professor Lankester tells me that about the time when a sort of jubilee was held in Schwann's honour at Liége in 1878, he was introduced to him, and ventured to ask in the course of conversation how it was that after the publication of his famous essay he had so long been silent. Schwann answered that he had not been idle, but that ever since he had been unsuccessfully occupied in trying to find out the secret of the constitution of the cell.

To return to the question propounded by Schwann, does the cause of organic phenomena lie in the organism or in its separate elementary parts, the cells? He answers very decidedly, in the separate elementary parts, and gives the following reasons for his answer: "All organised bodies are composed of essentially similar parts, namely, of cells; these cells are formed and grow in accordance with essentially similar laws, and therefore these processes must in every instance be produced by the same powers. Now if we find that some of these elementary parts not differing from the others are capable of separating themselves from the organism and pursuing an independent growth, we may thence conclude that each of the other elementary parts—each cell—is already possessed of the power to take up fresh molecules and grow, and that therefore each elementary part possesses a power of its own, an independent life, by means of which it would be enabled to develop itself independently if the relations which it bore to external parts were but similar to those in which it stands in the organism. The ova of animals afford us examples of such independent cells apart from the organism."

A little further on he says: "In inferior plants any given

cell may be separated from the plant and can grow alone. So that here are whole plants consisting of cells which can be positively proved to have independent vitality. Now as all cells grow according to the same laws, and consequently the cause of growth cannot in one case lie in the cell, and in another in the whole organism, and since it may be further proved that some cells, which do not differ from the rest in their mode of growth, are developed independently, we must ascribe to all cells an independent vitality, that is such combinations of molecules as occur in any single cell are capable of setting free the power by which it is enabled to take up fresh molecules. The cause of nutrition and growth resides not in the organism itself but in its separate elementary parts. . . . The manifestation of the power which resides in the cell depends upon conditions to which it is subject only when in connection with the whole organism."

The whole theory is very succinctly summed up in the following passage: "The elementary parts of all tissues are formed of cells in an analogous though very diversified manner, so that it may be asserted that there is one universal principle of development for the elementary parts of organisms, however different, and that this principle is the formation of cells".

No doubt objection may be taken to-day to the universality of this statement, but if we modify the last part of it and read "that the most general principle of development for organisms, however different, is the formation of cells," we shall have very nearly expressed the truth, as we know it at the present day.

I have found it necessary to quote Schwann's work at considerable length, and to repeat more emphatically what I stated in my previous essay on Epigenesis and Evolution.[1] Dr. Whitman,[2] in a reply which deals partly with my

[1] G. C. Bourne, "Epigenesis and Evolution," "SCIENCE PROGRESS," vol. i., 1894.

[2] C. O. Whitman, *Evolution and Epigenesis*. Boston: Ginn & Co., 1895.

criticisms, and partly with the much more weighty arguments brought forward at the same time by Dr. Oscar Hertwig, says that my criticisms, in so far as they are directed against the inadequacy of the cell-theory of development, are largely the result of misunderstanding; this may in part be true, but I cannot have misunderstood the simple meaning of his first paragraph, and I wish to insist on the fact that the cell-theory, as it was promulgated by Schwann, did *not* regard cell-formation as the whole secret of organic development, and that the cell was not, in the mind of the author of the cell-theory, the alpha and omega of both morphological and physiological research in the animal kingdom. If this is clearly understood at the outset, it will help to remove much possible misunderstanding.

But, as Mr. Sedgwick has rightly said, we have to deal not only with what its authors thought, but with the cell-theory as it is understood and taught at the present day. I have already pointed out[1] that the most recent definition of the cell-theory is, to all intents and purposes, identical with the broader generalisations of Schwann. Dr. Oscar Hertwig writes:[2] "Animals and plants, so dissimilar in their outward appearances, are similar in the essentials of their anatomical structure, since both are composed of similar elementary parts which for the most part are only recognisable by the microscope. . . . Since the cells, into which the anatomist resolves vegetable and animal organisms, are the bearers of the vital processes, they are, as Virchow has expressed himself, the vital units. Viewed from this standpoint the whole life process of a composite organism appears to be nothing else than the extremely complicated result of the individual life processes of its numerous and variously functional cells." This is simply a restatement in other words of two of the fundamental principles of Schwann, namely (1) that the elementary parts of all tissues are formed

[1] G. C. Bourne, "A Criticism of the Cell-theory," *Quart. Jour. Micr. Science*, vol. xxxviii., p. 137, 1895.

[2] O. Hertwig, *Die Zelle und die Gewebe*. Berlin: R. Friedlander und Sohn, 1893.

of cells; (2) that the cause of nutrition and growth resides not in the organism but in its separate elementary parts.

The attacks which have recently been directed against the cell-theory may be resolved into contradictions of these two fundamental propositions. On the one hand there is the considerable number of cytologists, whose opinions may be taken to be summed up in Whitman's essay on the inadequacy of the cellular theory, who deny the second proposition, and in so doing implicitly deny the truth of the first. They would say that the cause of nutrition and growth does not reside in the cells considered as elementary parts, but in parts still more elementary, the ultimate vital units of which the cells themselves are composed. On the other hand Mr. Adam Sedgwick denies the first proposition *in toto*. He states boldly that the elementary parts of tissues are not formed of cells, but of a continuous mass of vacuolated protoplasm containing nuclei.[1] These objections, though they are raised from different standpoints, are not irreconcilable, but it will be convenient to deal with them separately. First let us consider the objections to the cell as an ultimate vital unit.

These objections are of long standing. They were first brought forward by Brücke[2] in 1861;[3] not long afterwards

[1] Since this was written Mr. Sedgwick has published a further account of his views, which makes it necessary to modify this statement. See *infra*.

[2] Ernst Brücke, "Die Elementarorganismen," *Sitzungsberichte der K. Akademie der Wissenschaften*, Wien, bd., xliii., p. 381, 1861.

[3] Delage points out that the merit of regarding protoplasm as an organised substance belongs to Dujardin, and not to Brücke. At the same time he points out the essential difference between Brücke's concept of organisation and that of Dujardin, greatly to the advantage of the latter: "La difference entre Dujardin et Brücke est très simple. Le premier a deviné l'existence de *structures* que le microscope démontre aujourd'hui; tandis qu'en introduisant dans la conception de protoplasma cette notion acceptée avec enthousiasme, d'organismes très compliqués et invisibles, Brücke a ouvert la porte aux nombreuses théories speculatives qui cherchent á imaginer la structure de ces organismes pour expliquer par elles les phénomenes de la vie." Delage adopts the expression organisation, saying: "Le protoplasme n'est pas simplement, comme on l'a cru longtemps, une substance chimique *organique*, mais il est *organisé*, c'est-â-dire possede une

Herbert Spencer followed with his theory of physiological units. Darwin's theory of pangenesis expressed the same idea, and more recently Nageli, De Vries, Wiesner, Weismann and others have entered the same or at least similar objections to the cell-theory. Even Oscar Hertwig, although he appears in the sentence above quoted to give his adherence to the view that the cell is a vital unit, abandons this concept, for all practical purposes, in the latter part of his book; for he says, in a most unmistakable manner, that the cell is an organism composed of ultimate units which he calls idiosomes.

Each author whose name I have quoted has a somewhat different account to give of the ultimate constitution of the cell. But the points on which they disagree are of subordinate importance; they are all agreed on the main issue, that the vital activities manifested by the cell are not to be explained by the visible constitution and structure of the cell itself, nor by the mere chemical elements of which the protoplasm of the cell is composed. Each of them avers that the cell is *organised*, which means that it is made up of countless organic units of a lower order, differing among themselves, and arranged in groups and sub-groups within the cell in a manner analogous to that in which the cells themselves are arranged in a composite organism. Since there is so general an agreement in fundamental principle, I am spared the necessity of examining each separate theory of ultimate vital units in detail; should anybody wish for a condensed account of the various theories he will find it in Weismann's introduction to his work on the Germ Plasm.[1]

structure d'un ordre plus élevé que la structure atomique des molécules chimiques des composés organiques non vivants". No fault can be found with this definition, but would it not be better to adopt some other term to express this extra complexity of *structure* rather than "organisation," which is inseparably connected with our ideas of the composition of the bodies of higher animals and plants? For Brücke the organisation of protoplasm was the same in kind as the organisation of higher animals: for Dujardin it was something different, and had best be expressed by a different term. Delage puts the word structure in italics.

[1] Still better in Delage's book, referred to further on.

The point for present consideration is this: Is it necessary for the explanation of vital phenomena to assume the existence of ultimate vital particles, so minute as to be invisible with the best microscopical powers which we possess, each of which is to be considered as being *in posse* an independent organism capable of displaying some of the most characteristic of vital phenomena, *viz.*, assimilation, growth, metabolism, reproduction by division?

As it will be necessary to refer frequently to these assumed vital units, I must call them by some name, and I shall use Weismann's term biophor, without meaning to exclude the conceptions of other authors, the pangenes of De Vries, the plasomes of Wiesner and so forth. I use the term biophor in the sense of *Lebensträger*, the bearer of the vital properties, without necessarily implying that it possesses all the particular properties assigned by Weismann to his biophors.

Whatever the point from which the different authors have started, they all postulate the existence of minute biophors on the grounds that the vital phenomena exhibited by cells, say by an Amœba, or by the ovum of a Metazoon, imply the existence of an organisation adequate to the production of the observed processes. The life processes are too various and too complicated in their kind to be explained by the visible constitution of protoplasm, even if it be allowed, as it generally is allowed, that protoplasm is not a chemical compound of fixed molecular composition but a mixture of many chemical substances, each having a molecular composition of some considerable complexity. I have already shown that Schwann himself was possessed of such an idea, which he expressed sufficiently clearly when he referred to "a peculiar mode of union of the atoms to form atoms of the second order," but he did not attempt to follow out the idea, confining himself to the inquiry into "the arrangement of these conglomerate molecules when forming either the separate elementary parts of organisms or the entire organism". The term conglomerate molecule is in fact synonymous with the term biophor

in the sense in which I am using it, for the biophor or ultimate vital unit is held to be an aggregate of chemical molecules; the constitution attributed to it is that it is made up of many different kinds of molecules, just as a molecule may be composed of several different kinds of atoms. I shall have to refer again to the difficulties which still remain if we accept the hypothesis that a group of different molecules is able to exhibit the vital functions which are necessarily attributed to a biophor. Before proceeding to criticism I must try to give as fairly as I can the grounds for believing in the existence of biophors. To put the matter as briefly as possible, the theories of ultimate vital units are the result of attempts to make a mental analysis of living substance. Chemical analysis is impossible, for in the process the living substance is destroyed as such and becomes dead substance, possessed of different and much less important properties. One fact of great importance, however, is learnt from chemical analysis, and it was appreciated by Schwann, namely, that, to use his original words, "the elementary materials of organic nature are not different from those of the inorganic kingdom"; hence it has been inferred, with all reason, that the powers of organic nature are essentially the same as those of inorganic nature, and are established by the very existence of matter. It is only necessary to mention this because there has recently been a tendency in some quarters to call in the assistance of some mysterious "vital force"; a tendency begotten no doubt by the apparent futility of all attempts to find an explanation on mechanical and chemical principles of the fundamental powers of organic nature, assimilation and metabolism. This, however, need not detain us; we have to consider the process of reasoning which, in default of assistance from chemical analysis, has led so many distinguished observers and thinkers to analyse the cell into other components, and those again into others of a lower grade, until the biophor, the smallest particle of possible life, is reached.

The weightiest reason which I have been able to dis-

cover is given by von Sachs.[1] According to this author, whose views are in agreement with those of Nägeli on this subject, it is necessary for the explanation of certain phenomena exhibited by organic substances that we should assume the existence of combinations of molecules which form very large numbers of small particles or micellæ as Nägeli calls them. One of the most important of these phenomena is the imbibition of water. Dry organic substances, such as gelatine, when placed in water, imbibe it and increase in volume to a very considerable extent. The increase in volume produced by the swelling up in water is almost equal to the volume of water which has been absorbed. The imbibition of water in such a case is something very different from the imbibition of water by a porous inorganic body, such as gypsum, unglazed porcelain, etc. The latter substances are full of small visible and invisible cavities or pores, which in the dry state contain air. The water passes into these cavities or pores according to the laws of capillarity, and in so doing displaces the air, which is forcibly expelled and can be collected and measured; there is no pushing asunder of solid parts, as is shown by the fact that the porous body is not perceptibly enlarged by the water which has penetrated into it. But the water penetrating into gelatine expels no air, it does not enter by capillarity into spaces previously existent, but forces its way between the particles of the dry substance, pushing these asunder, and so causing the considerable increase in volume. The particles thus pushed asunder are the micellæ, and although they are pushed further apart from one another, they do not completely lose their connection. Each micella may be regarded as being surrounded by an envelope of water when in the moist state; in the dry state the micellæ composing the substance are in mutual contact. This familiar phenomenon of the swelling of organic substances by the imbibition of water is contrasted by von Sachs with the process of solution of a salt. In the latter case the water

[1] J. von Sachs, *Lectures on the Physiology of Plants*, translated by H. Marshall Ward. Oxford, Clarendon Press, pp. 205 and *sq.*, 1887.

seizes on the molecules of a crystal and takes them in between its own molecules; in the former case the dry organic body seizes on the molecules of water and forces them between its own. These reasons are held by von Sachs and Nägeli to be among the weightiest for regarding protoplasm as an "organised" body, in the sense of being made up of micellæ, and not as being a structureless slime or fluid.

No doubt they are weighty reasons for regarding organic substances such as gelatine, starch grains, cell walls, etc., as being composed of combinations of polyatomic molecules into groups of a higher order, and there is no objection to giving these groups a name, such as micellæ. But the admission that such groups exist does not really bring us much nearer to an explanation of the phenomena of life. Von Sachs himself points out that even in the region of pure chemistry it is necessary to assume that polyatomic molecules are grouped into closer molecular unions, thus giving rise to chemical properties which did not belong to the individual molecules.

Gelatine, starch grains and cellulose are not living but dead substances, and the fact that the behaviour of dead organic substance finds an explanation on a theory of micellar structure is but a very small step towards the explanation of the very different behaviour of living substance. The micellæ may exist in the organic substances in question, but they are not to be confounded with biophors; the very fact that the properties of dead substances may be attributed to their existence shows that they cannot be considered as bearers of vital properties.

In point of fact the living substance, which we generalise under the name of protoplasm, behaves quite differently in respect of the imbibition of water to the dead substances which are derived from it. An amœba or an infusorian, living in the water, does not imbibe it as a mass of gelatine would. But when it dies in the same water it immediately begins to swell up, and eventually bursts and disintegrates. So that we see that with respect to this very property which is held to be a reason for assuming a micellar structure of

protoplasm, the actual living substance does not exhibit the property, whilst the same substance when dead does. Clearly then, the admission that protoplasm has a micellar structure, that is, that it is composed of minute and invisible particles consisting of groups of polyatomic molecules, does not involve the admission that there are ultimate vital units, biophors, which reside in the cell-like organisms within the cell-organism. This distinction indeed has already been made and dwelt upon at some length by Weismann (*op. cit.*, pp. 41 and 42).

It follows then that whilst we may freely admit that protoplasm, and also various inert organic substances, are composed of micellæ, and are therefore "organised" in the sense spoken of by von Sachs, we have still to consider the evidence for the existence of biophors. At the outset of this inquiry we meet with a difficulty in that the existence of biophors is assumed by most authors as a means of explaining the phenomena of heredity, and this opens up a wide range of questions into which it is not the purpose of this essay to enter. But it has well been pointed out by Wiesner that if minute vital elements occur at all, those same units which make life possible, and control assimilation and growth, must also be the agents in bringing about the phenomena of heredity. This view, which commends itself to everybody, implies that the biophors have only secondarily acquired historic qualities, and that they are primarily concerned in the production of the fundamental processes of life. We may therefore dismiss for the present purpose the complications introduced by heredity and confine our inquiry to the functions of biophors as bearers of the essential vital qualities.

It is urged in favour of a theory of biophors that life must be connected with a material unit of some sort (Weismann); that function presupposes structure (Whitman), and that the structure necessary for the exhibition of such complicated functions as those of living protoplasm cannot be of such a simple molecular kind even as the micellar structure postulated by von Sachs and Nägeli, but must consist of a definite arrangement, an architecture or organ-

isation of separate living particles, the aggregate functions of which produce the vital phenomena. It is further urged in favour of this view of organisation, that in almost all cells we are able to recognise structures under the microscope each of which behaves in respect of growth and multiplication in a manner analogous to that in which the cell behaves. Not only the nucleus but also the chromatin bodies, the microsomata of which these are composed, the centrosomes, the green chromatophores of plant cells, may be observed to increase in size, *i.e.*, to grow and to multiply by division, and it is held that this is proof that the ultimate particles composing these bodies must assimilate, grow and divide in a manner similar to that in which cells assimilate, grow and divide.

This view, whilst receiving a considerable measure of support from other sources, has been most energetically supported by Wiesner,[1] whose extensive work on the subject has received the weighty approval of Weismann. Wiesner refers in detail to the various structures in the form of granules or corpuscles which may be observed in animal and vegetable protoplasm, and he attributes to one and all of them the powers of assimilation and multiplication by division. Nor does he confine himself to the living substance generally recognised under the name of protoplasm. He labours at great length to prove that the cell wall, so often considered as an inert non-living product of living protoplasm, is not in fact dead, but contains a living substance distinguishable under the name dermatoplasm, and ultimately composed of structural elements of the same fundamental nature as that of the cytoplasm. These ultimate particles are the *plasomes*, which form the central point of his theory of the constitution of living matter. Further than this he accepts in full the theory of De Vries with regard to vacuoles, and considers them to be just as much independent organisms as the chromosomes, the centrosomes, the chlorophyll bodies and other things. This theory of vacuoles, which

[1] J. Wiesner, *Die Elementar structur und das Wachsthum der Lebendem Substanz.* Wien: Alfred Hölder, 1892.

assumes that they are products of minute bodies called tonoplasts, is of itself improbable, and is contrary to the teaching of observations which may readily be made on the constitution and behaviour of vacuoles in living protoplasm. It has been shown by Bütschli[1] that the contractile and other vacuoles of Protozoa continually make their appearance without owing their origin to the division of previously existing vacuoles. It is not possible to go into details here, but the reader will find a full discussion of this question in Bütschli's work (p. 230) as also a *résumé* of the various theories which have from time to time been put forward on the subject of the granular theory of protoplasm. But even if peculiar views on the nature of vacuoles be laid aside, the gist of Wiesner's arguments is not materially weakened. None of the structures which are observable in protoplasm are observed to originate neogenetically: they are all, he says, derived directly by division from pre-existing structures of similar character. In short, he fully accepts the aphorism put forward somewhat earlier by Altmann: "Omne granulum e granulo". Wiesner does not definitely say that the various particles observable in protoplasm are to be severally identified with the ultimate vital units, his plasomes. Some of them may be individual plasomes, but the majority of them are, he thinks, aggregates of plasomes, units of a higher order which in turn are combined to form the still higher unit the cell. Thus he presents a scheme of organisation which, instead of taking the cell as the lowest structural unit, goes several grades lower; instead of the old conception of

organ—tissue—cell,

he represents the scheme of organisation as being

organ—tissue—cell—granules—plasomes.

A detailed criticism of Wiesner's views would occupy a much larger space than I have at my disposal, and such a criticism is unnecessary, since all that need be said has

[1] O. Bütschli, *Investigations on Microscopic Foams and Protoplasm*. Authorised translation by E. A. Minchin. London: A. and C. Black, 1894.

already been set forth by other authors in their criticisms of similar theories, particularly by Bütschli (*loc. cit.*, p. 195) and O. Hertwig, both of whom occupy themselves with Altmann's views, which are to all intents and purposes identical. Only a few of the most important points need be touched upon here.

It is certainly a remarkable fact, and confirmed by abundant experience, that many of the constituent parts of cells are produced by divisions which recall the divisions of the cell itself. The nucleus is the most important and the most familiar constituent of the cell: it is within the experience of every biologist that nuclei are never observed to originate neogenetically, but always by division of a pre-existing nucleus. The chromatin elements of the nucleus may be shown to be composed of minute particles, the so-called chromosomes, and these reproduce themselves by division, and are never observed to originate neogenetically. The same statement holds good for the centrosomes, for chlorophyll corpuscles and for various kinds of chromatophores. It is not to be denied that these facts, which become more and more familiar to the working microscopist, appear to lend a powerful support to the theory of biophors; in a limited sense they may be said to be a proof of the statement that the cell is an organised body. Whether, as Wiesner claims to be the case, there are many other constituents of cells which similarly reproduce their kind by division, and are never observed to originate independently, may for the present be left out of consideration. The evidence that amylum grains and granules of various kinds behave like the centrosomes in this respect, is as yet too slight, and the observations are too conflicting to enable us to come to a judgment without entering into a mass of detail which is not wholly relevant to the question at issue. But there is at least one criticism which is worthy of mention, namely, that of Bütschli, who points out (*loc. cit.*, p. 200) that among the strongly staining granules of protoplasm there are bodies which are not actually constituents of the protoplasm but are symbiotic micro-organisms. The existence of such organisms, which have been called

Bacteroids, has been frequently demonstrated in animal and vegetable cells, and Bütschli points out that granules similar in appearance to bacteroids occur in the Vorticellinæ and may be observed at certain times to be in a state of rapid proliferation.

Just before writing these pages I have been shown preparations exhibiting the numerous bacteria symbiotic in Pelomyxa, and it is very possible that the rapid proliferation of bacteroids has been mistaken by various observers for the reproductive activity of granules forming an integral part of the cell. It is almost certain that the mistake has been made in some cases, and until further investigation has increased our knowledge of the various micro-organisms which are symbiotic or parasitic in cells, it is well to be somewhat sceptical of statements regarding the divisional processes of cell contents. It would seem then that our present knowledge does not justify our regarding all the particles of a cell as originating in a similar manner from the division of pre-existent similar particles, though we must affirm in the most positive manner that some few of the constituents of the cell originate in this way only, and are never produced *de novo*. The question now to be considered is this: must we, because these bodies (the centrosomes, chromosomes, etc.) assimilate, grow and reproduce themselves by division, regard them as independent vital units? A cell exhibits these phenomena and the cell is regarded as an independent unit *in posse*, if not actually *in esse;* must we therefore attribute to all bodies exhibiting the same phenomena the character of independent units? The answer, I believe, is very decidedly no. Cells would never have been regarded as independent units if they had merely been observed to assimilate, grow and divide, whilst retaining their connection with other cells undergoing the same processes. The quotations which I have given from Schwann's work show that the theory that the cell is an independent life unit was not founded on the fact that it assimilates, grows and divides,—Schwann indeed overlooked the phenomena of reproduction by division—but upon the fact that cells are capable of

leading an independent existence. This is so important a part of the cell-theory that I may again quote in his own words Schwann's reasons for calling the cell an elementary unit of life. "Now if we find that some of these elementary parts not differing from the others are capable of separating themselves from the organism and pursuing an independent growth, we may thence conclude that each of the other elementary parts is already possessed of the power to take up fresh molecules and grow, and that therefore each elementary part possesses a power of its own, an independent life."

In the case which we are considering the very faculty which was so powerful a reason for regarding cells as independent units is wanting. Nobody has ever observed a nucleus or a centrosome or even a chromatophore to separate itself from the cell and pursue an independent existence. And not only is there no recorded case of the constituent particles of cells separating themselves spontaneously from the cell, but experiments which have been made with the express purpose of determining whether these particles can live apart from the cell to which they belong have in every case given a negative result. Even the nucleus, highly complicated as it is, and itself composed of smaller particles which may easily be demonstrated, perishes when removed from the cell body. The chromatophores similarly perish, and so no doubt would the centrosomes if it were possible to isolate such very minute particles. Many instances might be cited in proof of this, but it is scarcely necessary to bring forward the details; the reader can obtain them by reference to the works of Nussbaum,[1] A. Gruber and Verworn.[2]

It is of some interest in this connection to contrast the process of reproduction in unicellular and multicellular organisms. In the latter reproduction is effected by the separation of a single unit, a cell, from the aggregate, and

[1] M. Nussbaum, *Biol. Centralblatt*, vol. iv.

[2] Max Verworn, "Die physiologische Bedeutung des Zellkerns," *Pflüger's Archiv*, vol. li., 1892.

the unit so separated has from the time of its separation an independent individuality and eventually reproduces the aggregate. The fact that the union of two cells is commonly necessary for the maintenance of life and the exhibition of the powers of development, need not be urged as an objection to this simple statement of the case, for the facts of parthenogenesis show that the union of two cells is not an essential feature. Now if we adopt Wiesner's scheme, and imagine that organisation does not stop at the cell, but that beyond this there are granules, and beyond these again plasomes, and that the plasomes stand in the same relation to the cell that the cell stands to the multicellular organism; we should expect to find that in the reproduction of monocytial organisms the plasome plays a part analogous to that played by the cell in the reproductive processes of polycytial organisms. But we find nothing of the kind. The monocytial organism reproduces itself in just the same way as the polycytial, by the separation of a cell, complete in all its parts. There is no such thing known, even in cases where a flagellate or a radiolarian breaks up into innumerable particles or spores of extreme minuteness, as the separation of any one individual constituent of a cell possessed of the power of leading an independent existence and in time of reproducing all the other constituents. Every spore, however minute, has its portion of the cytoplasm and its share of nuclear matter. If there are any other constituents, it probably has its share of these also, but one cannot speak with certainty on this point, for positive evidence is wofully deficient. At any rate Wiesner, holding fast to his theory that nothing, not even an amylum or an aleurone grain, is produced neogenetically, is at great pains to prove that in cellular reproduction all the parts of the parent are transferred to the offspring. Assuming that this is so, and remembering that there is abundant evidence that nuclear matter and cytoplasm are always transferred, it is evident that the relation in which the plasomes or biophors, regarded as ultimate vital units, stand to the cell, is not at all the same as the relation in which the cell, regarded as an ultimate unit, stands to the

polycytial organism. Bütschli, in a short but very weighty sentence,[1] brings forward the same argument that I have just used in opposition to Altmann's theory of the part played by granules in the vital processes of protoplasm. In my judgment the argument as far as it goes is a sound one, but I am aware that it does not altogether refute the theory of biophors, but only that part of it which states that as cells are to polycytial aggregates so are biophors to cells. This refutation, however, seems to me to be a considerable gain. For it enables us to apprehend that the structure or constitution of the cell, whatever it may be, is not to be expressed in the same terms as the structure of the higher organisms.

It may be objected that nobody does express the structure of the cell in such terms, but the objection does not hold good. It is true that most authors are more guarded in their expressions than Wiesner, and evade the responsibility of declaring that the biophor is to the cell as the cell is to the polycytial organism, by means of reservations, couched for the most part in terms so ambiguous and even transcendental that the whole issue is involved in an obscurity from which it seems hopeless to try to escape. But these expedients are really of little use. The fact remains that in every case the fundamental idea is the same, that the phenomena exhibited by isolated cells having an independent individual existence are of essentially the same kind as the phenomena exhibited by polycytial organisms and must be explained on the same grounds.

If it be not so, what is the meaning of the argument which was first put forward in definite shape by Brücke, and has been repeated by every author who attacks the question in the same manner that he did, that the com-

[1] "So long as the individual constituents of the cell are not seen to persist when isolated, nor are distinct living phenomena observed in them, it is very dangerous to speak of their life as something which they possess in themselves. They are so far living, as long as the opposite is not proved, in that they are parts of living organism, so that the granula may be living in the same way as the nucleus, even though they no longer betray any sign of life after isolation" (*loc. cit.*, p. 199).

plexity of the phenomena exhibited by individual cells, say by an amœba, is so great, the functions observed are so many and so various in their kind that they can only be explained by the assumption that protoplasm is an organised body? Taking the words of O. Hertwig as a fair expression of current opinions on the life processes of a polycytial organism, "that the aggregate life processes of a composite organism appear to be nothing more than the exceedingly complicated result of the individual life processes of its numerous and variously functional cells," it is evident that to the minds of Brücke and his successors the aggregate life processes of the corpuscle of protoplasm called a cell are nothing more than the highly complicated result of the individual life processes of its numerous and variously functional biophors. If they do not mean this, I am quite at a loss to know what they do mean, or to understand the relevancy of the so-called axiom laid down by Whitman, that "function presupposes structure," or the meaning of the statement expressed so often and with such obvious satisfaction, that "the cell is an organism". These sentences, so terse and so epigrammatic, exercise a peculiar fascination over most minds. To understand their exact applicability to the question at issue they must be carefully examined. Function presupposes structure. To the biologist who makes a rapid mental survey of his experiences, this appears to be a generalisation of universal truth. Physiology, which draws its inferences almost exclusively from the study of the higher animals, tells us that ultimately every function of the composite organism is to be referred to a particular group of cells, and that cells differ in kind according to the different functions which they exhibit. So much is this truth forced upon us that if conceivably a new function were to make its appearance, we should immediately search for the cell groups appropriate to the performance of that function. So far so good, but before proceeding further we must take note that the statement that function presupposes structure is a generalisation founded on experience. It is not an axiom as Whitman calls it, for an axiom is a proposition which is self-evident, and this assuredly is not.

The next step is to transfer this generalisation, founded on experience, into a new region, to the functions of cells. In order to do this we should possess the same experiences with regard to the functions of cells which we possess with regard to the functions of composite organisms. But these experiences are entirely wanting. We observe that protoplasm exhibits functions, that it assimilates, that it is irritable, that it is contractile, that it is reproductive, and so forth; but who has been able to demonstrate or even to suggest with any plausibility that there are structures specially devoted to assimilation, to contractility, to irritability, and to reproduction in protoplasm? It is evident that the absence of any such experiences has been felt by many observers, who have accordingly studied protoplasm with a view to finding the required structures, and some are inclined to say that the nucleus or perhaps the centrosome is reproductive, the amylum and aleurone bodies are assimilative and so forth. But there are protozoa endowed with active functions which have no centralised nucleus; the presence of centrosomes has yet to be demonstrated in protozoa in general, and there are forms in which, as Bütschli well points out, the protoplasm is homogeneous, *e.g.*, in the pseudopodia *Gromia dujardini*.[1] The reader should refer to Bütschli's work for a discussion of the subject of hyaline protoplasm (*loc. cit.*, p. 262). The fact that it exists is of the highest importance, for it shows that there is living substance exhibiting the usual vital phenomena of assimilation, contractility, etc., which, nevertheless, defies all attempts to recognise an organisation which in the light of previous experience would seem adequate to the effects produced, and it shows also that the centrosomes, the amylum grains, and their analogues, and the whole category of granules are secondary phenomena, which may be

[1] Not only are there no granules in homogeneous protoplasm, but the alveolar structure of it is unrecognisable. It is easily shown, however, that the homogeneous substance is produced from alveolar protoplasm and is capable of reconversion into it. The physical explanation of the disappearance of the alveolar structure is given by Bütschli on p. 264 of the English translation of his work.

altogether absent and yet the life processes go on unchanged.

It must be confessed then, that the experiences which so amply justified our generalisation when applied to composite organisms are altogether lacking when we seek for a justification for applying it to the simplest unicellular organisms. Moreover I have just shown that in one important particular at least, we do not merely lack these experiences, but that we have experiences of an entirely different kind. In face of this is it not obvious that the captivating generalisation must be abandoned altogether in the region which we are now discussing? For it is founded on experience, and where experience fails or is contradictory the generalisation fails also.

After what has already been said it is unnecessary for me to enter into a detailed examination of the other statement which is considered to mark a great advance in biological thought, that "the cell is an organism". It is sufficient to say that if this proposition means anything at all, it means that the cell has an organisation which is similar in kind to that of a composite organism of which a cell is a part. If I am told that it does not mean this, but something else, then I ask, firstly, what does it mean? And, secondly, if it does not mean this, what necessity is there for assuming that the protoplasm of the cell is built up of biophors, the biophor being *the* elementary living constituent, assimilating, growing and dividing, taking up definite positions in the cell, combining with others like or unlike itself to form higher aggregates, and so impressing a fixed architecture on the cell of which it is a component? Why, in short, if the statement does not mean that the organisation of the cell is the same in kind as the organisation of a composite animal, why then does everybody who believes that the cell is an organism ascribe to it an organisation which is the same in kind as that of the higher animals?

The fact is, and it is patent to everybody, that most authors do conceive of the cell-organisation as being the same in kind as the organisation of higher animals. They either have the courage of their opinions, like Wiesner,

and say so in so many words, or they tacitly admit it by their description of what they conceive cell-organisation to be. They are dominated by the cell-theory. Mr. Adam Sedgwick has recently said that the cell-theory is an incubus which perverts the minds of biologists, whose minds are so saturated with conceptions borrowed from the cell-theory that they are unable to see anything else. I have elsewhere found fault with this statement, but when the theories of cell-organisation are considered, I must freely confess that he has right on his side. Not only does the zoologist believe "that the cell is the unit of structure, and that it forms the basis of organisation in the metazoa," but he also believes that some correlative of the cell forms the basis of all organisation whatsoever. His eyes are "blinded to the most patent facts" by ideas derived from the cell-theory, and it is not too much to say that the theory does "obstruct the way of real progress in the knowledge of structure". Whether consciously or unconsciously the believer in biophors starts with ideas derived from the cell-theory, he tacitly assumes the universal applicability of the proposition that function presupposes structure, and he seeks to explain the functions of protoplasm by attributing to it an organisation which in all essential characters is the equivalent of the organisation of the metazoa. Since I have just shown that there is no justification for transferring a generalisation based upon experience to a region in which experience is either wholly wanting or, if present, of a different kind, it is hardly necessary for me to elaborate and show that it is equally unjustifiable to attribute to the unknown a plan of organisation identical in kind with the plan which we have learnt by experience to recognise as the attribute of the known.

Some time ago I pointed out that there was a fallacy in the word organism.[1] Whitman has ridiculed the statement, yet the more I reflect upon it the more I am convinced that the fallacy exists, and that it is in the highest degree mischievous and misleading. By an organism we mean

[1] G. C. Bourne, "Epigenesis and Evolution," this journal, vol i., 1894.

either an independent living thing, in which case the term is loose but applicable to every animal in the monocytial stage, or we mean a thing possessing organisation, and by organisation we mean a certain structural plan, the idea of which is a generalisation from our experience of animal and vegetable structure in general. That this is historically and in fact the connotation of the term organisation is indubitable.[1] When we use the term organisation we either use it in this connotation or in some other. If we use it in the same connotation with respect to protoplasmic structure, we are consistent, but, as I have shown, we are applying ideas derived from one set of phenomena to another set of phenomena to which they are not appropriate. But if we use it with another connotation, then we expose ourselves at once to the risk of the well-known fallacy which is inseparable from the use of the same term with different connotations. If the two connotations are clearly defined and generally understood, the fallacy may be avoided, though the inconvenience remains; but if the one connotation is clear and definite whilst the other is vague and ambiguous in the highest degree, no amount of circumspection will prevent our falling into the fallacy almost at the first opportunity. This is exactly the case with the term organisation. In the one sense we know its connotation exactly, and when authors use it in that sense they have, in the course of their arguments, to adhere strictly to the technical sense of the word. Most of them do this, for they are aware of the absurdities and inconsistencies into which they would fall if they did otherwise. But what of those who use the term with another connotation? They assure us that it does not denote a plan of structure like in kind to that of the metazoa: what then does it denote? Something so vague, so unreal and unsubstantial that we

[1] Thus in Worcester's *Dictionary of the English Language*, 1881:—

Organisation. The condition of an organised body or the totality of parts which constitute and the laws which regulate an organised body.

Organised. Formed with organs: composed of several individual parts or organs, each of which has its proper function and conduces to the existence of the entire system.

are even at a loss to know to what to apply it; its connotation has never even been attempted. The futility of using a term without connotation and with the most vague denotation is so well illustrated by the following passage from Whitman that I cannot refrain from introducing it here: "When we speak of the organisation of the germ as cut directly from a pre-existing parental organisation of the same kind we are not thinking of the definitive organisation which belongs to the fully formed organism, but of that primary organisation which belongs to the protoplasm itself". This raises our expectations, we are going to hear something of the primary organisation which belongs to protoplasm itself. Whitman continues: "We are so accustomed to connect the idea of organisation with the anatomical organs of the adult that we are apt to forget that there is a primary organisation which underlies every anatomical organ. The germ has this primary organisation; it is therefore an organism, and as such may dominate its own development." From which weighty and sententious passage we gather that the germ is an organism because it has a primary organisation which is not the definitive organisation which belongs to the fully formed organism, but a primary organisation which belongs to protoplasm itself. What on earth, we may well ask, is this primary organisation? The answer is given on the same page. It is "that original constitution of the germ which pre-determines its type of development and the form which ultimately distinguishes it from other species developing under like external conditions". The terms "original constitution" and "primary organisation" are merely synonyms. So we learn that the primary organisation so important to those who have more thoughtfully scanned the gap between the cell and the physical molecule, is *the primary organisation of the germ*, which pre-determines its type of development, etc. I hope that others are satisfied by this most remarkable piece of scientific exposition. For myself I must humbly confess that I am none the wiser for it, any more than I should be if I asked what was a Megalosaurus and I was told: "A Megalosaurus, why you know it is a big lizard, it is—a—a

Megalosaurus in fact". Nor is confusion less when I am told in one sentence that the organisation of the germ cut directly from pre-existing parental organisation of the same kind is not the definitive organisation which belongs to the fully formed organism, but is that primary organisation which belongs to protoplasm itself, and I read in the sentence immediately preceding that "the essential thing is not simply continuity of germ substance of the same chemico-physical constitution, but actual identity of germ-organisation with stirp-organisation". The organisation of the germ is identical with the organisation of the stirp, and yet the organisation of the germ is not that of the fully formed organism, but is a primary organisation which belongs to protoplasm itself. What does it all mean? It is different and yet it is identical, and it is organisation, organisation, *toujours* organisation. I beg Dr. Whitman, for pity's sake, to descend from his altitude, scarcely dreamed of in the philosophy of Harvey and Wolff, and to condescend to inform a poor bewildered mortal, who confesses to a prejudice in favour of things which he can understand, what this wonderful primary organisation is.

Seriously speaking I believe that organisation either means a plan of structure of the same type as the structure of higher animals and plants, and capable of being described in intelligible terms as it has been by Weismann, Wiesner and others, or it means nothing at all; it is a mere phrase which seeks to cover but does not conceal our ignorance.

G. C. Bourne.

(*To be continued.*)

SOLID SOLUTIONS.

IF we define solutions as homogeneous mixtures of substances in variable proportions, we are at once obliged to admit the existence of solid solutions, for there are many mixed solids which fulfil the requirements of this definition. Common potash alum, for example, can crystallise together with ammonia alum, and form mixed crystals which are perfectly homogeneous and of the same composition through out, although the proportions of the two constituents may be varied at will by proper selection of the aqueous solution from which the crystals separate.

We are inclined, however, to look in solutions for something more than mere homogeneity and uniformity of composition, and perhaps one of the most obvious characters of a liquid solution is this, that should it at first be of different composition in different parts of its mass, there is always present the tendency of the dissolved body to attain a uniform distribution throughout the solvent. The process of equalisation of the composition, or diffusion, occurs in all solutions which are more concentrated in one part than in another, the dissolved substance moving from the place of greater to the place of less concentration. Diffusion in solution goes forward very slowly if the liquid is protected from mechanical disturbance and sudden change of temperature, months being requisite for the attainment of uniform concentration if a comparatively short column of pure solvent is placed above a denser layer of strong solution contained in the bottom of a cylinder. If diffusion takes place in solids we might expect it to proceed even more slowly.

A class of substances which form in some sort a connecting link between liquids and solids, and are specially suited to the study of diffusion phenomena, is to be found in jellies. Graham, to whom we owe our first exact knowledge of diffusion in liquids, prepared a stiff jelly containing common salt in solution in one part, and compared the rate at which

the salt diffused in it with the rate at which salt diffused in pure water. He found that the diffusion in the jelly took place almost, if not quite, as fast as in water itself. The composition of the jelly was 2 per cent. gelose and 98 per cent. water, so that, as far as actual substance was concerned, the salt had to meet practically the resistance of water alone in both cases, and the experiment showed that the mere change in apparent condition of the whole mass had little or no influence on the rate of diffusion. Subsequent experiments have served to confirm Graham's results.

When we pass to solids proper we find that instances are not wanting of what is apparently diffusion within them. Van't Hoff in his fundamental paper on solid solutions gives numerous examples. In the preparation of steel by the cementation process bars of wrought iron are packed in charcoal and subjected to a red heat for several days. The charcoal gradually penetrates the iron and converts it into steel. It matters little for our purpose what the particular form is that the carbon assumes during its passage through the iron—in some fashion or other it reaches the centre of the dense bar. The distribution of the carbon, too, if the operation is interrupted before uniformity has been attained, is precisely what would be expected if the phenomenon were one of real diffusion ; and the influence of time is the same in both processes. Not only has carbon been observed to pass through iron, but it has even been proved to travel slowly through porcelain, when porcelain crucibles have been heated in a bed of graphite.

When a metal such as copper is deposited galvanically on another metal, it penetrates beyond the surface of the latter into its substance, and zinc objects which have been lightly coppered are, even when protected by a coating of varnish, occasionally observed to become white again owing to the gradual mixing of the two metals near the surface.

Professor Spring, of Liége, who has devoted special attention to the chemical behaviour of solids under high pressure, has supplied some interesting instances of pheno-

mena which can only be explained by the assumption of solid solutions. When equivalent proportions of barium sulphate and sodium carbonate are finely powdered, intimately mixed, and subjected to a very high pressure, a double decomposition takes place with formation of barium carbonate and sodium sulphate. The decomposition, however, is not complete, only 20 per cent. of the original substances being transformed. If, on the other hand, we start with a mixture of barium carbonate and sodium sulphate and compress it, we find that the reverse transformation now occurs, barium sulphate and sodium carbonate being formed, and that to the extent of 80 per cent. of the original substances present. Here we are evidently dealing with a state of equilibrium between the four substances above mentioned, which can only exist together permanently under pressure in certain definite proportions. If these proportions are departed from, the system so transforms itself that the requisite state for equilibrium is attained. Now this of itself points to the substances existing here in a state analogous to that of bodies in liquid solution, for we know that in general definite proportions are necessary in solutions for stable equilibrium to exist. In the case of solids the general rule is that when they are in equilibrium under given conditions in one proportion, they are in equilibrium under the same conditions in every other proportion. The behaviour, then, of these solids under pressure is analogous to the behaviour of substances in solution, and different from the ordinary behaviour of solids. The continuance of the pressure is not essential to the establishment of such a definite solid equilibrium, for Spring has shown that by relieving the pressure after 73 per cent. of a system of barium carbonate and sodium sulphate had been transformed, the process continued, though less rapidly, and after a week had reached the proportion of 80 per cent. necessary for equilibrium. Here diffusion must have played a part, for no matter how finely divided the reacting substances originally were, their surface of contact (where alone the mutual decomposition could take place if there were no diffusion) must have been comparatively small.

It is well known that some metals have the property of allowing certain gases to pass through them under favourable conditions, the most thoroughly investigated instance of this kind being the permeability of the metal palladium to gaseous hydrogen at moderately high temperatures. At about 300° C. hydrogen can pass quite freely through a palladium septum, and it is difficult to conceive the nature of this phenomenon without admitting the existence of diffusion in the solid. Whether the hydrogen is dissolved in the palladium or forms a compound with it, as has been asserted, is of little consequence, for in the latter case the compound superficially produced must have possessed the power to penetrate the remaining metal, or to allow of the passage of hydrogen through itself.

Connected with the process of diffusion in solution we have the phenomena of the conduction of electricity in solutions, or electrolysis. Here the electric current is carried by material particles, and the resistance that these experience in their passage through the solution is of the same nature as the resistance offered to diffusion. Helmholtz, in his Faraday lecture, drew attention to the fact that glass behaves as an electrolyte towards an electric current, *i.e.*, that the current in passing through the glass is associated with two currents of particles moving in opposite directions. The particles travelling towards the negative pole of the battery have since been proved to move faster than those moving towards the positive pole. Lehmann also has shown that when two silver electrodes are immersed in fused iodide of silver, which is afterwards allowed to solidify, and a current of electricity is passed through the solid iodide, one of the electrodes increases in weight at the expense of the other, and that the phenomenon can be reversed by reversing the current.

These examples will suffice to indicate that we are not without data to establish an analogy between the behaviour of certain solids and the behaviour of ordinary liquid solutions. Since the appearance of van't Hoff's original paper on the subject a considerable number of researches have been published more or less directly bearing on the question,

but the results achieved have on the whole been small, owing chiefly to the experimental difficulties encountered.

An important application of the idea of solid solutions was made by van't Hoff in explaining the abnormalities that are sometimes met with in the determination of molecular weights by the lowering of the freezing-point in solutions. It had been proved theoretically that the freezing-point of a given solvent should be depressed to a certain value (calculable from the freezing-point and the latent heat of fusion of the solvent) when the solution was of normal concentration, *i.e.*, contained one gram-molecule of dissolved substance per litre. The nature of the dissolved substance should be without influence on this value. Now, whilst it was ascertained experimentally that this theoretical relation was in the vast majority of cases accurately fulfilled, yet there remained certain combinations of dissolved substance and solvent which gave values of the depression constant altogether at variance with the calculated value. Thus, metacresol dissolved in phenol gave a depression of 48 instead of 74, and thiophene dissolved in benzene a depression of 34 instead of 53. Van't Hoff's explanation of these and similar abnormally low values of the depression was that the freezing-point observed was not in the strict sense the freezing-point which had been assumed in the theoretical reasoning. The true freezing-point of a solution is the temperature at which the liquid is in equilibrium with the *solid solvent*. The freezing-point of an aqueous salt solution, for example, is the temperature at which it can exist in contact with pure ice without the ice melting or without fresh ice being deposited from the solution. Now, in the exceptional cases above alluded to it is known that the solid and the solvent have a tendency to crystallise together, *i.e.*, to form mixed crystals, so that the substance that separates out is not the pure solvent but rather a solid solution. The temperature at which such a solid solution would be in equilibrium with the liquid solution might not by any means be the freezing-point of the solution as above defined. The apparent observed freezing-point of the solution, therefore, would not in general coincide

with the calculated depression, and van't Hoff from theoretical considerations showed how the divergence could be estimated from a knowledge of the composition of the solid which actually separated out from the solution on cooling. That the abnormal values for the points of solidification depend on the separation of the dissolved substance along with the solvent has now been experimentally verified in a considerable number of cases. Heycock and Neville found that for the case of solutions of antimony in molten tin, the freezing-point of the tin was raised instead of lowered by the presence of the second metal. Küster has shown that this and similar instances are susceptible of a very simple explanation. The two metals separate out together in very nearly the same proportion as that in which they remain behind in the liquid, so that the solution solidifies as a whole. In such circumstances the point of solidification of the liquid can be calculated by the simple mixing formula. If the melting-point of each pure substance is multiplied by the proportion in which it exists in the mixture, the sum of the two numbers thus obtained will give the point of solidification of the solution. As antimony melts 200 degrees higher than tin, the admixture of the former in however small proportion will, since the mixture freezes as a whole, raise the point of solidification instead of lowering it, as would be the case if pure solid tin separated from the liquid on cooling.

Not only do solutions exhibit a lower freezing-point than that of the pure solvent, but they also exhibit a lower vapour tension. The pressure of aqueous vapour over salts containing water of crystallisation may in many cases be measured with accuracy, and there it is found that the isomorphous admixture of another salt lowers the vapour pressure of water which is in equilibrium with the solid. Thus the vapour tension of a mixed crystal of ordinary alum with iron alum is less than the vapour tension of either of its components. In this respect then the mixed crystal behaves as a solid solution. Again, the solubility of a substance is diminished when it itself acts as a solvent for another substance insoluble in the original solvent. Of the

three liquids, ether, water, and benzene, ether and water are partially miscible, benzene and water are immiscible, and ether and benzene miscible in all proportions. Suppose we take water as the original solvent—then on shaking it up with ether we find that the latter dissolves to a certain definite extent in it, *i.e.*, possesses a certain solubility in water. If now we previously dissolve benzene in the ether which we shake up with the water, we find that the water will now take up less ether than before. The solubility of ether in water is thus diminished when benzene is dissolved in it—and this behaviour is characteristic of all such combinations of substances.

A case of this kind where two solids play the part of the ether and benzene in the previous instance has been thoroughly studied by F. W. Küster. The solid hydrocarbon naphthalene is, like the hydrocarbon benzene, insoluble in water; β-naphthol, on the other hand, is, like ether, sufficiently soluble in water to permit of accurate estimation. But naphthalene and β-naphthol can crystallise together in any proportion so as to form a complete series of isomorphous mixtures, the melting-points of which vary according to the rule given above for mixtures of antimony and tin. A comparison of the amount of β-naphthol dissolved by a given quantity of water from such mixtures led to somewhat unexpected results. Instead of the addition of a small quantity of naphthalene to β-naphthol lowering the solubility of the latter in water, it was found that mixtures containing as much as 30 per cent. of naphthalene had precisely the same solubility as β-naphthol itself. As more naphthalene was added the solubility increased slightly, afterwards to diminish continuously to zero as the mixture was made to contain more and more naphthalene. The explanation of this behaviour suggested by Küster is that naphthalene and β-naphthol are capable of forming a chemical compound consisting of one molecule of each substance, this compound being decomposable by water, an assumption by no means improbable, as many similar cases have been observed. If we allow further that the solubility of the compound is greater than the solubility of β-naphthol, the

results are satisfactorily accounted for. The diminution of solubility when much naphthalene is present is the normal depression of the solubility of the compound by the addition of excess of naphthalene. The solubility greater than that of pure naphthol is the solubility of the compound naphtholnaphthalene. The constant solubility (equal to that of β-naphthol) observed when there is little naphthalene in the mixture is the solubility of β-naphthol, for the naphthalene in the mixture is in the form of the compound naphtholnaphthalene, which is decomposed at the surface by water into naphthalene and β-naphthol, which exist now alongside of each other and not in the intimate union of a crystalline isomorphous mixture.

In connection with the results of these experiments Küster is inclined to make a distinction between crystalline isomorphous mixtures and solid solutions proper, because in the former there is practically no diffusion owing to what may be termed the rigidity of the crystalline structure. He admits, however, that no absolutely sharp line can be drawn, as there are various intermediate degrees in which diffusion may take place. A reference to the examples of diffusion in solids previously cited in this paper will show that they all occur in amorphous bodies without any regular structure.

A point of considerable interest in the theory of solid solutions is that it affords us the possibility of determining molecular weights of the dissolved substances, and since in isomorphous mixtures we usually attribute similarity of molecular structure to the two components, we can also in this case form an estimate of the molecular weight of the solid solvent. From his experiments on the amount of β-naphthol dissolved by water from mixtures of that substance with naphthalene, Küster was able to calculate with a high degree of probability the molecular weight of each of these substances in the solid state. In the first place he found that with mixtures containing excess of naphthalene the ratio of the square root of the concentration of β-naphthol in the solid mixture to the concentration in the aqueous solution saturated by that mixture was very nearly constant,

varying but little with the actual composition of the mixtures taken. The general theory of solutions asserts that when a substance (here β-naphthol) is divided between two immiscible solvents (here water and naphthalene, or naphtholnaphthalene) it will be distributed in a constant ratio between the two solvents, no matter what amount of it be taken, provided only the molecular weight of the substance is the same in both solvents. In the case investigated this does not hold—the ratio of the concentrations in the two solvents is not constant; and the molecular weight of β-naphthol dissolved in water is therefore different from the molecular weight of β-naphthol "dissolved" in naphthalene. The theory further asserts that when, as in the present instance, the concentration in one of the solvents is proportional to the square root of the concentration in the other solvent, the molecule in the second solvent must be twice as great as the molecule in the first. We know that β-naphthol dissolved in water has the normal molecular weight corresponding to the formula $C_{10}H_8O$; in naphthalene solution it has consequently the molecular weight corresponding to the formula $(C_{10}H_8O)_2$.

The theory of solutions likewise enables us to calculate the molecular weight of the naphthalene in the above experiments from the diminution of the solubility of the β-naphthol in water as it dissolves more and more naphthalene. In the case before us the question is slightly complicated by the existence of naphtholnaphthalene molecules, but Küster was able to arrive at the result that naphthalene must have double the molecular weight in the state of solid solution that it has in the state of vapour, *viz.*, $(C_{10}H_8)_2$.

Another well-investigated case of solid solutions is that offered by the absorption of hydrogen by palladium. Troost and Hautefeuille, in order to obtain information as to the state in which the hydrogen existed within the metal, made an extensive series of observations of the pressure of hydrogen in equilibrium with palladium containing different amounts of hydrogen. They found that with compositions of the solid up to one atom of hydrogen to two atoms of palladium the pressure of hydrogen remained constant

at 100° C., after which it increased rapidly as the proportion of hydrogen in the solid increased. The analogy between this case and the case of the solubility of mixtures of β-naphthol and naphthalene in water is at once apparent. In both instances we have constancy of pressure (gas-tension) and solubility (solution-tension) within a certain range of composition, and then rapid variation with further change of composition. The conclusions arrived at in both instances are also similar. The constant solubility was attributed by Küster to the formation of a compound naphtholnaphthalene—the constant tension was attributed by Troost and Hautefeuille to the formation of a compound Pd_2H, in which any excess of hydrogen was then absorbed. Quite recently, however, grave doubts have been thrown on the existence of this compound. A very careful repetition and extension of Troost and Hautefeuille's experiments by C. Hoitsema has proved that the constancy of tension observed by these investigators was not absolute but only approximate, and that under slightly varying conditions the apparent constancy disappeared altogether. It would seem, therefore, that no compound of palladium and hydrogen is formed when the gas is absorbed by the solid, the state of the hydrogen being rather one of simple solution in the palladium. A comparison of the concentrations of the hydrogen above the palladium and of the hydrogen in the palladium indicates that at very low pressures the hydrogen in the metal exists as molecules only half as great as those of the gas, *i.e.*, as molecules consisting of only one atom. At higher pressures the concentration of the free gas and that in the palladium stand in a nearly constant ratio, from which it is to be inferred that the molecule of hydrogen in the metal, as well as the molecule of gaseous hydrogen, is represented by the formula H_2.

A problem which has long interested chemists is the determination of the nature of the process involved in dyeing. Some contended that the process was one of chemical union of the dye with the substance of the fibre, others that it was merely one of mechanical absorption. In 1890, however, O. N. Witt propounded a new theory which, on account of

its plausibility, met with a ready acceptance in many quarters.

According to Witt the state of the dye-stuff in the fibre is one of solid solution, and many analogies were advanced in support of this assertion. For example, dyed materials show the colour, not of the solid dye-stuff, but of the dye-stuff in solution, when there is a difference of colour between the two states. Solid fuchsine is green, its aqueous solutions are red, and so also are materials dyed with it. The dye-stuff rhodamine in the solid state exhibits no fluorescence, in solution it does, and silk dyed with rhodamine is fluorescent likewise. The theory of Witt thus appeared very promising as an explanation of the phenomena of dyeing, but a closer investigation has shown that it cannot be accepted unconditionally, although some modification of it may be found to satisfy the experimental requirements. It has been proved in a considerable number of instances now investigated that the concentrations of the dye in the dye-bath and in the fibre do not stand to each other in a relation of simple proportionality, but the concentration in the bath is roughly proportional to a power (usually 3 to 5) of the concentration in the fibre. Now on the theory of solid solutions this indicates that the molecule of the dye in the water is three to five times as great as the molecule of the dye in the silk; but this cannot be the case, for the molecule of the dye-stuff in aqueous solution can be shown by other means to be the simplest possible. The numbers rather indicate analogy to the process known as absorption from solution. Substances like animal charcoal and platinum black have the property of condensing gases in the extensive surface they present. Similarly they can abstract certain substances from solution, as may be seen in the employment of animal charcoal for the decoloration of solutions. The relation between the concentration in the solution and that in the charcoal proves to be of the same kind as is met with in dyeing, so that we are led to suspect a similarity in the nature of the two processes. The so-called "iodide of starch," the blue compound formed when starch and iodine solution are brought into contact, would

appear to be a substance of the same nature as a dyed fibre and as charcoal saturated with an acid from solution, for the concentrations of the iodine in the aqueous solution and in the starch obey approximately the same law as in the other instances.

We are therefore forced to conclude that whatever success has attended the application of the theory of solid solutions to other processes, the theory can scarcely without modification be accepted as giving an explanation of the process of dyeing.

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JAMES WALKER.

THE STELAR THEORY; A HISTORY AND A CRITICISM.

PART I.

IN the study of the histological anatomy of plants, apart from the structure of the individual cell, the greatest advances of the last two decades have been made rather by the establishment of new points of view than by the discovery of new facts. Twenty years ago the solid foundations of the subject had been securely laid, and a considerable portion of the imposing fabric of histological detail which now rests upon them had already been built up. This fact is most clearly brought out by the masterly summary of existing anatomical knowledge published by De Bary in 1877. But splendid monument as it is of its author's unsurpassed knowledge of his subject, there can be few who have not felt that the *Vergleichende Anatomie* is, as a whole, essentially unreadable. Compare it, in imagination, with Sachs' *Vorlesungen* or with Haberlandt's *Physiologische Pflauzenanatomie*, and we are forced to recognise that De Bary's work is rather an encyclopædia than a piece of great scientific literature. The cause is to be found in the simple fact that there did not exist in 1877 a philosophy of the morphological aspect of the subject capable of informing "an epitome of the present knowledge of 'the Anatomy of the Vegetative Organs of Vascular Plants,'" as the idea of adaptation informed the works of Sachs and Haberlandt.

It is nothing less than the establishment of such a philosophy that we now owe to the great Frenchman, Van Tieghem. The most important part of his ideas is contained in what we may call the Stelar Doctrine of Vascular Tissue, and it is with this that we shall here be exclusively concerned.

Although the foundations of the stelar theory were laid many years ago, outside France it has made its way very slowly. In Germany even now it is apparently ignored

by the majority of anatomists, notwithstanding its acceptance by the most brilliant of German contemporary investigators.

In England, though these ideas have recently been made familiar to the student by more than one of our leading botanists, their discussion has still the interest of comparative novelty. And although the general idea of the stele as a morphological unit is simplicity itself, yet the application of this idea is in some cases by no means easy, so that not only does Strasburger's interpretation of certain facts differ from Van Tieghem's, but the author of the theory has himself been led to modify his original views in an important manner. The possibility of such a difference in the interpretation of facts which are undisputed seems to spring, if we may say so without presumption, from a certain want of definiteness in the apprehension of the criteria legitimate to their interpretation.

To investigate these criteria and to endeavour to ascertain their relative validity is one of the primary objects of the present paper.

We shall begin with an account of the development of the stelar doctrine.

HISTORY OF THE STELAR DOCTRINE. FIRST PHASE—THE IDEA OF THE CENTRAL CYLINDER.

In 1870-1, Van Tieghem published, in the *Annales des Sciences Naturelles*, a memoir (1) which was to have been the first of a series entitled "Recherches sur la symétrie de structure des plantes vasculaires". This instalment consisted of a general introduction setting forth the plan of the whole work, followed by 274 pages devoted to an extended anatomical account of the root, in vascular plants.

The introduction is of the greatest interest. The author tells us how he wished to obtain anatomical definitions of root, stem, and leaf, in order to give a basis to the study of comparative anatomy. These definitions are to be framed in accordance with the different kinds of symmetry exhibited in the arrangement of the vascular strands in the three organs, to each of which a separate memoir

is to be devoted. The results so obtained are to be applied, in a further series of memoirs, to the solution of a number of morphological problems, such as the true nature of tendrils, tubers, spines, phylloclades, ovules, etc., and finally, to the elucidation of the laws of symmetry governing the structure and relations of the ideal colony that would be formed if every seed germinated *in situ*.

This elaborate scheme for "un cercle d'études anatomiques complets et fermés" enables us to understand the strength and the weakness of the author's stelar theory. The imperative desire to reduce the anatomy of vascular plants to a perfect system depending upon simple laws of symmetry governing the arrangement of the vascular tissue, has been the means of giving us a doctrine, luminous indeed, and of wide significance, but scarcely of that rigidly universal application which its author claims. But here again, as is so often the case in the history of science, the attempt to work out logically the various implications of such a theory, has been of the utmost value in clearing our ideas and extending knowledge, not only by stimulating to the discovery of new facts, but by forcing us to examine the foundation of our conceptions.

Of Van Tieghem's scheme, as it stood in 1870, however, only the first memoir, that on the root, was ever written. The author demonstrates the fundamental identity of structure in the roots of all vascular plants, and obtains his anatomical definition based on the symmetry of the vascular system. He shows that the vascular tissue of a young root forms a central cylinder which contains near its periphery "faisceaux libériens" (phloems) alternating with "faisceaux vasculaires" (xylems) united by "cellules conjonctives". Hence the vascular system is symmetrical in relation to a *line*, which is the organic axis of the organ. The stem agrees with the root in this last point, but on the other hand has its "faisceaux libéro-vasculaires," "réunis directement par le parenchyme primordial". Where the main root passes into the main stem there occurs a "cessation du tissu conjonctif spécial, qui se trouve remplacé par le parenchyme primitif". This sentence is specially interest-

ing because it shows that when it was written Van Tieghem had no idea of a central cylinder in the stem.

Two years later, however, in 1872, in describing (2) the transition from root to shoot in *Tagetes patula*, he writes how the "membrane protectrice" (endodermis) is continued up into the stem, retaining its characteristic thickenings, and immediately internal to it the "membrane rhizogène" of the root (later named the *pericycle*) is also found in the stem still giving rise to rows of lateral roots, one row arising from each interval between two bundles. Opposite the bundles, however, he holds that the "membrane rhizogène" is interrupted, since here the endodermis abuts directly on the group of fibres capping the bundle, fibres which in accordance with the current opinion he considered to belong to the phloem. Here then we have the first clear description of the continuation of the central cylinder of the root into the stem, and the idea of this continuation is the fundamental idea of the stelar theory. It is most clearly expressed in a note on p. 112, "Ainsi, et j'insiste sur ce point, la tige est, comme la racine, et dans toute son étendue, composée d'un cylindre central et d'un parenchyme cortical limité en dehors par un épiderme, en dedans par une membrane protectrice ou endoderme".

The generality of this condition is further insisted upon: "Le caractère sur lequel je viens d'appeler l'attention se retrouve dans la tige de la grande majorité des plantes vasculaires, mais il souffre pourtant quelques exceptions. M. Caspary a montré, en effet, que dans quelques plantes (*Minyanthes trifoliata, Adoxa moschatellina, Brasenia peltata*) chaque faisceau constitutif de la tige est individuellement entouré par une membrane protectrice à cellules plissées ('Bemerkungen über die Schutzscheide,' in *Pringscheim's Jahrbücher*, 1865-66, iv., p. 101). J'ai retrouvé le même fait sur quelques autres plantes, notamment sur *l'Hydrocleis Humboldtii*. Dans ce cas, il n'y a pas non plus de membrane rhizogène dans les entrenœuds de la tige, et il n'existe aucune solution de continuité, aucune distinction réelle entre le parenchyme cortical et la moelle" (p. 113). This paragraph shows clearly that thus early

Van Tieghem had recognised the condition which he afterwards described as "astely".

The "membrane rhizogène," now considered, under the name of pericycle, as forming merely the external layer of the conjunctive tissue of the cylinder, was at that time treated as a region external to, and distinct from, the rest of the parenchyma, to which the name "conjonctif" was given. But the clear recognition of the existence of an individualised stem cylinder, forming a direct continuation, tissue for tissue of that of the root, was the first and fundamental step in the evolution of the stelar idea.

Little progress was made during the next ten years in the development of this conception.

Falkenberg (3), in 1876, showed that the "Aussenscheide" in monocotyledonous rhizomes corresponds with the "pericambium" in roots, both in position and *rôle;* and Mangin (4) in 1882 entirely confirmed his results and showed that not only adventitious roots but also the "réseau radicifère" arises from this layer, which he calls the "couche dictyogène".

In 1882 Van Tieghem published a short paper (5) in which, *à propos* of the Cucurbitaceæ, he gives conclusive reasons, based upon grounds of comparative anatomy, for regarding the fibres in the stem, hitherto called primary "bast fibres," as really belonging to the "membrane rhizogène". With these extended limits, this layer forms a complete investment of the stem cylinder, just as the pericambium does of the root cylinder. Since the one layer is the direct continuation of the other, and the two correspond very largely in function as well as in position, it is clearly desirable that they should have a common name. For this purpose Van Tieghem introduced the word *pericycle*, which was to supersede the various terms "pericambium," "Aussenscheide," "membrane rhizogène," "couche dictyogène," etc., applied by various writers to the same layer in various plants and parts of plants, according to its various histological characters and functions. The importance of this introduction of the conception of the pericycle was of course very great, since it fixes more accurately the external

limit of the cylinder, and thus brings into greater prominence the idea, already clearly stated in 1872, of an individualised stem cylinder in direct continuity with that of the root.

The term has eventually, though very slowly, found its way into general use.

In 1884 Morot, a pupil of Van Tieghem, published the results of a research (6) devoted to a comparative investigation of the pericycle in both root and shoot.

The publication of Morot's paper brings to an end what we may call the first phase in the development of the stelar idea.

SECOND PHASE—POLYSTELY AND ASTELY.

The second phase was inaugurated in an investigation (*7a*) by Van Tieghem and his pupil Douliot, of the anatomy of the stem of various species belonging to the genus Primula. Their observations were carried out on a number of new species from the East, as well as on many old species, making together a total of 114. They resulted (*7b*) in a division of the aggregate genus *Primula* L., into two segregates, *Primula* Tourn. and *Auricula* Tourn., as had been already done by Tournefort, but now based on a fundamental difference in the structure of the stem of the two segregate genera. While the stem of the species belonging to *Primula* possesses a single normal central cylinder in its whole extent, the narrow cylinder of the hypocotyl of an *Auricula*, instead of dilating in the ordinary way above the level of the cotyledons, gives rise by successive bifurcations to two or more vascular strands, each surrounded by an endodermis and possessing the structure of the single hypocotyledonary cylinder. In the genus *Gunnera* (*Haloragea*) a similar state of things obtains. These facts were, in the main, already known, having been investigated by Vaupell, Kamienski and Reinke. The opinion of these authors was, however, that the separate vascular strands were vascular bundles of the "concentric" type with peripheral phloem, comparable for instance to those found in the cortex of certain *Melastomaceæ*; and this was the view

taken by De Bary in his classical *Vergleichende Anatomie*. The numerous vascular strands in the rhizomes of most Leptosporangiate Ferns were regarded by De Bary in the same light.

But Van Tieghem, having, as we have seen, come to regard the central cylinder rather than the bundle as the morphological unit of vascular tissue in both root and shoot, was now led to the conclusion that in *Auricula*, *Gunnera* and the majority of Ferns[1] we have really to deal with a splitting of the single cylinder of the hypocotyl, as we trace it upwards, by successive bifurcations, into a number of such cylinders (7*c* and 8). Van Tieghem and Douliot proposed to call such a cylinder a *stele* (Greek στήλη, a column). A root or a stem containing one such stele would be *monostelic*, if it contained more than one *polystelic*. A third case was distinguished. If the cylinder of the hypocotyl breaks up, as it is traced upwards, into its component bundles, each of which is surrounded by a special endodermis, the cylinder, according to our authors, no longer exists; the stem is *astelic*. This case, already described in 1872, obtains in the stems of various *Ranunculaceæ*, in *Nymphæaceæ*, in *Hydrocleis*, in some species of *Equisetum*, etc., as well as in the majority of petioles and in blades of all leaves.

Cases of Polystely fall into two groups. First, where on a transverse section the various steles are seen to be completely separate, we have a state of *dialystely*. Secondly, where the steles are united laterally, so as to form a more or less complete ring in transverse section, enclosing a more or less isolated portion of extra-stelar tissue, which occupies the centre of the ring, we have a state of *gamostely*. These two conditions are not to be sharply separated, since the steles of all polystelic stems show more or less frequent lateral unions, and the gamostelic condition is simply a case where these unions are very frequent and persistent.

[1] Leclerc du Sablon in 1890 (9) worked out the connections, in several Ferns, of the single hypocotyledonary cylinder with the cylinders of stem.

We may tabulate the results thus obtained as follows:—

Monostely.—A single central cylinder. All roots and hypocotyls, nearly all Phanerogamic stems, and stems of many Vascular Cryptogams.

Polystely.—More than one cylinder. Stems of most ferns, most species of Selaginella, and among Phanerogams of *Auricula* and *Gunnera.*[1]

(*a*) *Dialystely.*—Steles separate for most of their course. Most Ferns *Selaginellæ* and. *Auricula ursi*, etc. *Gunnera.*

(*b*) *Gamostely.*—Steles united laterally for most of their course. *Marsilia*, *Pilularia*, *Pteris aurita*, etc. *Auricula japonica*, etc.

Astely.—No cylinder. Leaf blades, most petioles, stems of some species of *Equisetum* and *Ranunculus*, stems of *Hydrocleis*, *Ophioglossum*, *Limnanthemum*, *Nymphæaceæ*, etc. (7*c*).

The publication, in 1890-91, of the second edition of Van Tieghem's *Traité de Botanique* (10), which contains a full exposition of the stelar doctrine on the lines indicated, may be said to mark the close of the second phase in the development of the theory.

THIRD PHASE—EXTENSIONS AND MODIFICATIONS.

The third phase, from that date to the present time, has been occupied by various developments and modifications of the doctrine on the part of the author and his pupils, and has been marked by considerable criticism, mainly of these newer developments.

The first line of research that calls for notice is a re-investigation of the conjunctive tissue of the typical central cylinder of the flowering plant. This has led Flot (11) to

[1] In a paper recently communicated to the Linnean Society, Mr. B. G. Cormack describes cases of polystely met with in the adventitious roots of three genera of Palms, *viz.*, *Areca*, *Cocos* and *Verschaffeltia*. It appears that the single stele of the root splits, as it is traced downwards, into a ring of separate steles. Later on these steles again pass over into a single cylinder. This seems to be an important modification of Polystely as described by Van Tieghem and Douliot, and Leclerc du Sablon.

add a new region to those already distinguished. He finds a zone situated at the periphery of the pith, *i.e.*, just internal to the ring of bundles, corresponding exactly to the pericycle external to the ring, as well characterised histologically as the pericycle itself, and indeed resembling the latter very closely in structure and *rôle*. This zone, the *perimedullary zone*, is according to Flot (and his figures entirely support this) separate in development from the pith proper, or *internal conjunctive*, and belongs rather to the hollow cylinder of tissue (the "thickening ring" of the older German anatomists) giving rise to the bundles and the conjunctive immediately surrounding them (*external conjunctive*). It is impossible sharply to separate the perimedullary zone on the one side, just as Morot found it impossible to separate the pericycle on the other, from the ray tissue, and we should rather regard the contrast of the pith with the external conjunctive tissue, as of greater importance than the division of the latter into pericycle, rays and perimedullary zone, which are in the main *topographical regions* marked out by the limits of the bundles. In many adult stems it is however impossible to fix the limits of external and internal conjunctive, just as it is often impossible to fix the limits between external conjunctive and cortex. Flot is of opinion that this is owing to a growth in breadth of the cells of the external conjunctive continued longer than in the pith, the whole of the tissue of the cylinder thus becoming approximated in size and shape. This same cause, together with a masking of the endodermal thickenings (in cases where these are originally present) by a general thickening of the walls of all the parenchyma cells may very conceivably account for the frequent absence of the obvious limit between cortex and cylinder, though we are not aware that such an occurrence has been either established or suggested.[1] Further investigation on this point, as well as on the separation of the regions in root cylinders with a well-developed con-

[1] I now find that Sanio (24, pp. 371-2) states that this is practically what occurs in the stem of *Ranunculus acris*.

junctive system, is much needed to complete our knowledge of these matters.

An important modification of the theory of steles has been made by Van Tieghem himself in extending the use of the term astely so as to make it include the state of things obtaining in the stems of all species of *Equisetum* (12), and of *Ophioglossaceæ* (13).

Let us take first the case of *Equisetum*. Well-marked endodermes are found in the stems of all species, but their disposition, which was fully worked out many years ago by Pfitzer, is very various, not only in different species, but in different parts of the stem of the same species. There are three types of arrangement. In the first each vascular bundle is surrounded by a special endodermis; in the second the ring of bundles is bordered within and without by a general endodermis; and in the third the outer endodermis alone is present. In the second edition of the *Traité* Van Tieghem assigned the first two conditions to the astelic, the third to the monostelic type, but in a paper (12) published in the same year (1890) he calls attention to the fact, discovered by Pfitzer, that *all the species possess, at their nodes, the first or second of the arrangements in question.* He therefore concludes that all belong really to the astelic type, and that where, for instance, the second type, just above a node, passes back into the third, we have simply a case of the disappearance of the special characters of the inner endodermis, *which must still be supposed to exist.* The "monostely" is only apparent, and the tissue bordering the central canal of the stem, internal to the inner (theoretical) "endodermis," is not in reality pith, but rather "inner cortex" (extra-stelar tissue). The first of the three arrangements is to be called *dialydesmic*, since each bundle with its sheath of conjunctive is separate; the second and third *gamodesmic*, since the conjunctive tissue surrounding the bundles is in lateral confluence.

Turning now to the *Ophioglossaceæ* we have a similar argument (13). The stem of *Ophioglossum vulgatum*, below the level of the first leaf, is monostelic, but above the

first leaf contains five separate bundles each with a separate, though feebly suberised, endodermis. Hence it was treated by Van Tieghem, in the *Traité*, as astelic. In *Botrychium Lunaria*, whose stem is also monostelic at the base, the endodermis, after the departure of the first leaf trace, does not close round each separate bundle but becomes as it were invaginated into the cylinder, so that the vascular tissue forms on transverse section a horse-shoe bounded by the endodermis. The free edges of the horseshoe meet, as we pass up the stem, and the inner portion of the endodermis becomes entirely separated from the outer, so that we have an equivalent of the second or gamodesmic condition found in the stems of *Equiseta*. Higher up the inner endodermis loses its thickenings, just as in some *Equiseta*, and this gives us an apparently monostelic condition. In accordance with his revised view, Van Tieghem considers that *Ophioglossum* has an astelic-dialydesmic stem, while those of *Botrychium* and *Helminthostachys* are astelic-gamodesmic.

THE STATUS OF THE STELE CRITICISM.

It will be most convenient to introduce here a critical investigation of the stelar theory as thus modified by its author, and so far as it depends upon the morphological interpretation of the arrangement and relations of vascular tissue in the adult organs of vascular plants; deferring for the present a consideration of the developmental facts bearing upon the theory.

There is no need to discuss at any length the fundamental conception of the stele arrived at in the period which we have called the first phase of development of the idea. It depends upon the tracing into the stem of the root cylinder, and upon the demonstration that its characters as a cylinder are maintained in the latter. This demonstration, begun, as we have seen, in 1872, eventually led to the explicit recognition of the fact that the system of bundles forming the central cylinder possesses morphological characters much more constant than those of the vascular bundle,

and is hence more worthy to be taken as the morphological unit of vascular tissue. It is indeed impossible to give a morphological definition of a vascular bundle at all. "From the very first those bundles which consist essentially of definitely arranged groups of tracheæ and sieve tubes . . . have been called *vascular bundles*" (14, p. 232, Eng. ed.). But thus defined, a "vascular bundle" has no constant histological characters beyond the fact of containing both xylem and phloem. According to the arrangement of these, bundles have been classified as radial, concentric, collateral, etc. Such an arrangement brings together vascular strands of very different orders of complexity. In the first place it associates the axial cylinder ("radial bundle") of a root, possessing a number of quite distinct xylem and phloem strands, with the "collateral bundle" of a Phanerogamic stem, formed of a single strand of xylem and phloem in close association, the latter being continuous moreover with a portion only of the former. Again it associates even more closely under the term "concentric bundle" the vascular strands found in the stem of *Auricula*, *Gunnera* and Ferns with those of quite different structure found in the pith and cortex of *Melastomaceæ*, etc.

Such a classification is clearly, from a morphological point of view, quite artificial. But if we extend the use of the term bundle, as is often done, so as to include strands of tracheæ alone, and of sieve tubes alone, we can retain it as a convenient word without morphological connotation, and applicable to any strand of tissue belonging to the vascular system. And we may then qualify the word by any adjective we choose without morphological implication. Thus we may speak of the composite radial bundle of the root as composed of separate xylem bundles and phloem bundles alternating at its periphery; of the concentric bundle of the stem of an aquatic plant as sometimes composed of separate collateral bundles, in other cases consisting simply of a continuous cylinder of phloem surrounding a central strand of xylem; of the concentric bundle of a fern petiole gradually passing to the collateral type as we trace it into the lamina, and so on. Meanwhile the study of the homologies of the

various strands is quite a distinct matter, and requires a distinct terminology.

THE BOUNDARY OF THE STELE.

The acceptance of the central cylinder in the "monostelic" stem as a region of the first morphological rank is now very general. The only criticism which we have to consider is that which calls attention to the frequent want of definiteness about its external limit, and is inclined on this ground to question its individuality. This want of definiteness arises from the absence, in many adult stems, of the special characters of the endodermis (innermost layer of the cortex), often combined with an identity in size, shape and characters of cell-membrane between the cells of the cortex and those of the conjunctive. Such a state of things obtains, to take a single instance, in the stem of *Ranunculus repens*. A transverse section of such a stem shows the separate bundles imbedded in a homogeneous ground tissue, and to speak of a well-marked central cylinder is to speak of that which does not, in fact, exist.

Now this, as it stands, is a perfectly legitimate criticism, and its force as against the general validity of the stelar idea depends simply upon the greater or less generality of the condition described. Van Tieghem (10, p. 752) states that when, after the formation of the endodermis, the stem undergoes considerable intercalary growth, the folds on the radial walls of the endodermal cells become stretched out so that they become difficult or impossible to see. In other cases no suberisation of the radial walls occurs, and then, unless the endodermal cells are distinguished by possessing starch, it is admitted that the limit of the cylinder is difficult to determine, but says Van Tieghem (*loc. cit.*): "il reste la forme différente des cellules". This, however, as has been said, is by no means always obvious. A possible cause of such a condition, assuming the limits of the *young* cylinder to be well defined, has already been suggested, but new investigations are necessary to determine the point. If, for the sake of argument, we make the opposite assump-

tion, that the vascular bundles are sometimes differentiated in the middle of a homogeneous ground tissue, no trace of a special endodermis or pericycle being visible at any time, we could not predicate the existence, *in such cases*, of a central cylinder in the stem. And further, if such a condition obtained in the majority of instances (certainly an unlikely supposition) we should not, of course, be justified in predicating the *general* existence in the stem of a central cylinder, and this would necessitate such a radical modification in the generalised statement of the facts, that the stelar idea would lose the greater part of its significance. We shall have to recur to a discussion of the limit of the cylinder, but these simple considerations are insisted upon here, because they are apparently lost sight of in much of the current writing of Van Tieghem's adherents. It seems to be implicitly assumed that if a good anatomical distinction can be made in a certain number of cases, it is permissible to generalise the distinction and erect it into a morphological doctrine. The existence of those cases to which the doctrine does not apply is either ignored, or the distinction is said to be "theoretical". There is of course no such thing as a true "theoretical" distinction which is not also actual. The fallacy arises from a tendency to regard all morphological doctrine as of absolute value, whereas its value is never anything but relative. What we have to decide in any given case is the *amount* of this relative value, and whether that amount is sufficient to make the doctrine express a general truth so far as the objects under consideration are concerned.

The foregoing reflections lead us naturally to consider those cases which Van Tieghem himself excepts from the application of the stelar doctrine, namely, the cases of "astely". Already in the earliest paper containing the germ of the stelar idea we find certain cases not covered by the general statement of the existence of a cylinder in the stem. In 1886 these cases together with other similar ones were called astelic, and more recently still the conception has been further elaborated.

The conception is governed throughout by the idea of the endodermis as a definite morphological layer, always separating stelar from extra-stelar tissue. And the endodermis is to be recognised by the suberised thickenings on its radial walls. It is simply by the disposition of layers of cells so thickened that we are supposed to be able to distinguish the various arrangements described. It is easy to show that this criterion is quite illegitimate. The term endodermis is defined by Van Tieghem as the innermost layer of the cortex which "offre fréquemment" the special character in question (10, pp. 738-9). Not only, however, do cell layers with the same character occur in quite other situations (*e.g.*, in the middle of many periderms), but the innermost layer of the cortex certainly does not always possess it. So that these thickenings cannot be used to mark a layer of invariable morphological value. And even in *Equisetum*, Van Tieghem does not keep to his own criterion. For when the "astelic gamodesmic" passes to the apparently monostelic condition we are told that the inner endodermis is still present though its special characters have disappeared. But, we may well ask, if such great importance is to be attached to these special characters as to justify us in founding new types of structure simply upon the disposition of the layers exhibiting them, why should we be suddenly asked to recognise as equivalent a layer which does not exhibit them? The criterion becomes completely chimerical.

Strasburger (15) has pointed out that an endodermoid layer is an air-tight barrier which does not prevent the passage of water through its cells. Such a layer is found in a position to shut off the water-conducting system of a plant from its air-containing lacunar system, but this position may vary within the same genus (*Ranunculus*, *Equisetum*), and has no necessary connection with any morphological region. As a matter of fact it is most often formed from the inner layer of the cortex, but may be developed from conjunctive tissue, or even (leaf of *Isoetes*) from intra-fascicular parenchyma. Since the innermost

layer of the cortex does not always possess the special thickenings which give it the right to be called a "membrane," Strasburger objects to Van Tieghem's redefinition of the word endodermis, and proposes to substitute the term *Phloeoterma*, to be applied to the inner layer of the cortex, *i.e.*, to be used in the strictly morphological sense, whether this inner layer has special characters or not, and to reserve the term endodermis in accordance with its original sense for any sheath or membrane composed of cells with suberised radial walls or other distinctive thickenings, without reference to its position. This revised terminology certainly helps us to get rid of the confusion of thought manifested in Van Tieghem's use of the word endodermis. Strasburger concludes that as all species of *Equisetum* agree in possessing a ring of simple collateral bundles, they should all be considered monostelic, whether the phloeoterma be developed as a general endodermis, or each bundle possess a special endodermis, the phloeoterma having no characters by which it can be distinguished. The same considerations would apply to the genus *Ranunculus* and the other cases of "astely". While we must fully admit the general force of his argument on the ground of comparative anatomy, it is difficult to agree with the following sentence: "Die Grenze der Rinde gegen den Centralcylinder ist dort wo sie sich nicht besonders als Endodermis oder Stärkescheide markirt, nur theoretisch zu ziehen, dieselbe ist aber für alle Fälle festzuhalten" (15, p. 484). How is one to "hold fast" a limit which one cannot distinguish? We can only refer to the remarks which have been already made upon this subject, but we shall briefly recur to the subject in considering the development of the stele.

Leaves furnish us with excellent examples of the frequent impossibility of separating stelar from extra-stelar tissue. Putting aside those cases in which one or more steles from the polystelic stem directly enter the petiole (*Gunnera*, Ferns), we have to consider the ordinary case in a flowering plant, where we have one or more bundles leaving the cylinder and passing into the petiole.

These bundles are accompanied by a certain amount of closely associated parenchyma belonging to the external conjunctive of Flot, a tissue which in the leaf Van Tieghem now calls *peridesm* (16). The bundles are sometimes arranged in a ring, and the whole may be, though comparatively rarely, surrounded by an endodermis. The petiole is then, according to Van Tieghem (10, p. 842), monostelic. In the commoner case where each bundle has an endodermis of its own the petiole is astelic.

Strasburger prefers the term *schizostelic* (15), since the stelar tissue of the petiole represents a separated *portion* or portions of that of the stem. To such a portion he gives the name *schizostele* or *schistostele*[1], at the same time denying the existence of monostelic petioles in Phanerogams on the ground that the apparent pith of the petiole is continuous with the cortex, and not with the pith, of the stem. This last contention brings forward a difficult position. Is it desirable to introduce the question of continuity at all? If we have in the petiole a structure apparently identical with that which we have agreed to call monostelic in the stem, should we be satisfied to call it monostelic here also, without considering the connections of its parts with those of the stem? The strength of Strasburger's position lies in the fact that the continuity, region for region, of the cylinder of root and stem is really the basis of the stelar idea. The origin of the difficulty is to be found in the tendency of a petiole, where it is subject to the same conditions as a stem, to assume the characters of a stem, and among them the arrangement of its vascular tissue according to a radially symmetrical type. We might, perhaps, fitly call such a structure a *pseudostele*.

The mesophyll of the leaf (corresponding with the cortex of the stem) which surrounds the smaller vascular bundles, often has its innermost layer or phloeoterma, which abuts

[1] Van Tieghem has since (17, p. 285) used the word *meristele* for Strasburger's "schizostele," and applied the latter term to the portion of stelar tissue enclosed by each special endodermis in an "astelic" stem. This seems an unwarrantable diversion of the meaning of Strasburger's term.

immediately upon the peridesm of the bundle, specially characterised. The cells of the phloeoterma are often deprived of chlorophyll, or this is confined to the side walls, and these walls may also be suberised. It is, however, a rare case for such layers to be united in a continuous system with the phloeoterma of the stem, and thus to shut off completely, by means of a continuous membrane, the entire stelar system of the plant from its cortical tissue. This state of things obtains, however, in *Pinus* and some dicotyledonous genera, *e.g.*, *Galium*. In most dicotyledonous petioles endodermoid layers, if distinguishable at all, are often incomplete and not necessarily formed from the phloeoterma. A closed sheath to the bundles is, however, often formed in Angiosperm petioles by thickened peridesmic (stelar) tissue, such a sheath being called by Strasburger a *stelolemma* (15). The *ensemble* of the phenomena shows us, clearly enough, that the endodermis, in its original sense, cannot be taken here, any more than in the stem, as a layer of constant morphological value. The phloeoterma may be distinguishable by endodermal or other characters, but on the other hand, it may not.

The main fact in regard to the vascular system of the leaf is one which was pointed out by Van Tieghem in 1870. The system is bilaterally symmetrical in relation to the plane including the organic axes of both leaf and stem, and not, like that of root and stem, radially symmetrical about its organic axis. The designation of the continuous cylinder of root and stem as a *stele* and of each bundle or the whole bundle system of the leaf as a *schistostele* or *meristele* is in complete accord with this general fact. But we must not disguise from ourselves that both the stele and the meristele may not exist in the adult as sharply separated structures.

A. G. Tansley.

(*To be continued.*)

ON SOME APPLICATIONS OF THE THEORY OF OSMOTIC PRESSURES TO PHYSIOLOGICAL PROBLEMS.

PART II.

IN my previous article I gave some account of a research by Heidenhain in which this observer, after drawing certain deductions from the theory of osmotic pressures, shows that the phenomena of absorption from the intestinal canal are irreconcilable with these deductions, and are therefore not susceptible of a mechanical explanation, but must be ascribed to the active intervention of cells. Since analogous problems to those discussed by Heidenhain are continually coming before us in physiology, it is important that we should have a clear idea of the factors which are involved in the passage of water or dissolved substances across membranes. I therefore propose to reproduce Heidenhain's statements, and then to consider how far they are true for the special cases which occur in the body.

These statements are as follows :—

1. If two watery solutions with the same osmotic pressure are separated by a membrane through which diffusion can take place, no change in volume occurs on either side of the membrane.

2. If the solutions on either side of the membrane are of unequal osmotic pressure, water passes from the side where the pressure is less to the side where the osmotic pressure is greater.

3. The osmotic pressure of a solution is equal to the sum of the partial pressures of the various dissolved substances.

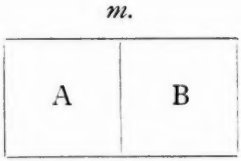
4. If the solutions on the two sides of the membrane have the same total osmotic pressure but unequal partial pressures of their various constituents, each constituent of the solution passes from the side where it has the higher partial pressure to the other side. No change in the volume of water on the two sides takes place.

Of these four statements only one (No. 3) is absolutely

correct. The other three are only correct under certain defined conditions which are rarely fulfilled in the body. There are factors at work which have been practically disregarded by most of the recent workers on the subject, and which may tend to produce movement of fluid in apparent opposition to the difference of osmotic pressure. Instances of such cases are afforded in a paper by Lazarus Barlow, to a consideration of whose work we shall shortly return.

There can be no doubt that in the phenomena of transference of fluid or dissolved substances across a membrane the nature of the membrane itself is all-important. I will, therefore, shortly run through the various modes in which interchanges may take place across membranes of varying permeability. We shall see that the close analogy which exists between substances in solution and gases, when dealing with "semi-permeable" membranes, is also borne out by experiment when used to predict the behaviour of solutions separated by such permeable membranes as occur in the body.

The simplest case is that in which two fluids are separated by a perfect semi-permeable membrane that permits the passage of water but is absolutely impermeable to dissolved substances. In this case the transference of water from one side to the other depends entirely on the difference of osmotic pressure between the two sides.



If we suppose two vessels, A and B, separated by such a membrane, A containing a solution of α and B a solution of β, water will pass from A to B so long as the osmotic pressure of β is greater than the osmotic pressure of the solution of α. If B be subjected to a hydrostatic pressure greater than the osmotic difference between the two fluids, water will pass from B to A until the force causing filtration or transudation (the hydrostatic pressure) is equal to the

force causing absorption into B (the difference of osmotic pressures). Under no circumstance will there be any transference of salt or dissolved substance between the two sides. Such semi-permeable membranes as this, however, rarely occur in the body. It is possible that the external layer of the cell-protoplasm may in some cases resemble the protoplasmic pellicle of plant-cells in possessing this "semi-permeability"; but in nearly all cases where we have a membrane made up of a number of cells, it can be shown that such a membrane permits the free passage of at any rate a large number of dissolved substances.

Let us now consider what will occur when the two solutions A and B are separated by a membrane which permits the free passage of salts and water. If the osmotic pressure of B be higher than A at the commencement of the experiment, the force tending to move water from A to B will be equal to this osmotic difference. But there is at the same time set up a diffusion of the dissolved substances from B to A and from A to B. The result of this diffusion must be that there is no longer a sudden drop of osmotic pressure from B to A, and the result of the primary osmotic difference on the movement of water will be minimised in proportion to the freedom of diffusion which takes place through the membrane. Now let us take a case in which A and B represent equimolecular and isotonic solutions of α and β. It is evident that the movement of water into A will vary as $A\not{p} - B\not{p}^1 = O$. But diffusion also occurs of α into B and of β into A. Now the amount of substance diffusing from a solution is proportional to the concentration, and therefore to its osmotic pressure, as well as to its diffusion coefficient.

Hence the amount of α diffusing into B will vary as $A\not{p} . \alpha k$ (when k is the diffusion coefficient).

In the same way the amount of β diffusing into A will vary as $B\not{p}, \beta k'$.

Hence if αk is greater than $\beta k'$, *i.e.*, if α is more diffusible than β, the initial result must be that a greater number of

[1] $A\not{p}$ = osmotic pressure of A, etc.

molecules of α will pass into B than of β into A. Hence the solutions on the two sides of the membrane will be no longer equimolecular, but the total number of molecules of $\alpha + \beta$ in B will be greater than the number of molecules of $\alpha + \beta$ in A, and this difference will be most marked in the layers of fluid nearest the membrane. The result therefore of the unequal diffusion of the two substances is to upset the previous equality of osmotic pressures. The layer of fluid on the B side of the membrane will have an osmotic pressure greater than the layer of fluid in immediate contact with the A side of the membrane, and there will thus be a movement of water from A to B. Hence if we have two equimolecular and isotonic solutions of different substances separated by a membrane permeable to the dissolved substances, there will be an initial movement of fluid towards the side of the less diffusible substance.

We have an exact parallel to this in Graham's familiar experiment in which a porous pot filled with hydrogen is connected by a vertical tube with mercury. In consequence of the more rapid diffusion outwards of the hydrogen than of atmospheric air inwards, the pressure within the pot sinks below that of the surrounding atmosphere, and the mercury rises several inches in the tube. We must therefore conclude that even when the two solutions on either side of the membrane are isotonic, there may be a movement of fluid from one side to the other with a performance of work in the process.

The experimental proof of the truth of this argument is to be found in a recent paper by Dr. Lazarus Barlow. This observer—after pointing out that the huge total osmotic pressures of the salt solutions in the body can very seldom come into play—insists on the fact that the most important point to study in this regard is the initial changes that take place between dissimilar fluids separated by a membrane—as he terms it—the initial rate of osmosis. For this purpose he employs a funnel, the neck of which is prolonged into a capillary tube, while on the mouth is tied a piece of peritoneal membrane. The funnel is filled with the solution whose osmotic attraction for water it is wished

to measure, and its mouth covered with the membrane is immersed in distilled water or in dilute serum.

The experiments which are the most interesting are those in which decinormal solutions of glucose, urea, sodium chloride were compared as to their initial rates of osmosis, the outer fluid being water. He concludes from his experiments that, in the case of prepared peritoneal membrane, the initial rates of osmosis of glucose, sodium chloride and urea in equimolecular solutions do not correspond to the ratio between their final osmotic pressures (as estimated by the depression of freezing-point), but the initial rate of osmosis of glucose (*i.e.*, the rate with which water passes into this solution) is greater than that of sodium chloride, and the initial rate of osmosis of sodium chloride greater than that of urea.

In these experiments the only two solutions which are strictly comparable are those of urea and glucose ($\Delta = 0{\cdot}189°$ C.), since the decinormal Na Cl solution had nearly double the osmotic pressure of these two ($\Delta = 0{\cdot}351$). In three typical experiments, each of which lasted three hours, the average rates at which the fluid in the funnel increased in volume during the first hour were: in the case of glucose, $7\frac{1}{8}$ mm. in five minutes; in the case of sodium chloride, $4\frac{3}{8}$ mm.; and in the case of urea, $1\frac{5}{24}$ mm. These figures are evidently not proportional to the difference of osmotic pressures between the fluid and the funnel and the water in the reservoir. But we have already seen that the moving force is not the total difference of pressure between the fluids in the vessels on either side of the membrane, but the difference of pressure between the layers of fluid in immediate contact with each side of the membrane. The fall of osmotic pressure across the thickness of the membrane varies inversely as the rate of diffusion of the dissolved substance. The question arises therefore whether the results obtained by Lazarus Barlow can be accounted for by differences in the rate of diffusion. In the carefully worked-out tables by this observer we have all the data necessary to decide the question. In the case of glucose, the freezing-point of the solution at the begin-

ning of the experiment was – 0·189° ; at the end of the three hours' experiment it was – 0·177° C.—corresponding to a loss of 6 per cent. of the dextrose. In the case of the urea, the freezing-point at the beginning was ·189°, and at the end was – 0·154° C., a loss of 18 per cent. Here then the initial rate of osmosis of the glucose was about five times that of the urea ; the loss by diffusion of the glucose was about one-third that of the urea. In the case of the sodium chloride the loss amounted to 22 per cent. ; but here the total difference of osmotic pressure was very nearly double that of the other two solutions, and the result is that the initial rate of osmosis of the sodium chloride takes an intermediate place between that of urea and that of glucose.

In this paper the results of another experiment are given to show that osmosis may occur from a fluid having a higher final osmotic pressure *towards* a fluid having a lower final osmotic pressure. If, for example, equimolecular solutions of sodium chloride and glucose be separated by a peritoneal membrane, the osmotic flow will take place from the fluid having the higher final osmotic pressure—sodium chloride. We might compare with this experiment the results of separating hydrogen at one atmosphere's pressure from oxygen at two atmospheres' pressure by means of a plate of graphite. In this case the initial result will be a still further increase of pressure on the oxygen side of the diaphragm—a movement of gas against pressure taking place in consequence of the greater diffusion velocity of hydrogen.

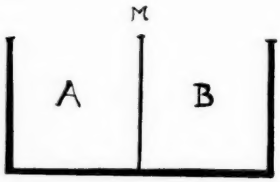
So far we have only considered the behaviour of solutions when separated by a membrane, the permeability of which to salts is comparable to that of water ; so that the passage of salts through the membrane depends merely on the diffusion rates of the salts. There can be no doubt, however, that we might get analogous movements of fluid against total osmotic pressure determined, not by the diffusibility of the salts, but by the permeability of the membrane for the salts—a permeability which may depend on a state of solution or attraction existing between membrane

and salts. We have a familiar analogue to such a condition of things in the passage of gases through an india-rubber sheet. If two bottles, one containing carbonic acid, the other hydrogen, be separated by a sheet of india-rubber, CO_2 passes into the hydrogen bottle more quickly than hydrogen can pass out into the CO_2 bottle, so that a difference of pressure is created between the two bottles, and the rubber bulges into the CO_2 bottle. We might, in the same way, conceive of a membrane which permitted the passage of dextrose more easily than that of urea. With such a membrane, experiments conducted in the same way as Dr. Barlow's, would lead to diametrically opposite results. The importance of the membrane in determining the direction of the osmotic passage of fluid is well illustrated by Raoult's experiments. When alcohol and ether were separated by an animal membrane, alcohol passed into the ether, whereas if vulcanite were employed for the diaphragm, the osmotic flow was in the reverse direction, and an enormous pressure was set up on the alcohol side of the diaphragm.

Here we have a possible clue to the "explanation" of many phenomena of cell activity, to which the term "vital" is often assigned. In the swimming-bladder of fishes, for instance, we find a gas which is extremely rich in oxygen, and the oxygen is said to have been secreted by the cells lining the bladder. It is, however, very possible that the processes here may be exactly analogous to Graham's atmolysis, and that the bladder may represent a perfected form of Graham's india-rubber bag.

The next point to be considered is the passage of a dissolved substance across membranes in consequence of differences in the partial pressure of the substance in question on the two sides of the membrane. Great stress is laid by Heidenhain and his pupil Orlow on the fact that in the peritoneal cavity, as well as from the intestine, salt may be taken up from fluids containing a smaller percentage of this substance than does the blood plasma, and they regard this absorption as pointing indubitably to an active intervention of living cells in the process. This argument

requires examination. Supposing the two vessels A and B to be separated by a membrane which offers free passage to water, and a difficult passage to salts. Let A contain ·5



per cent. salt solution and B a solution isotonic with a 1 per cent. Na Cl, but containing only ·65 per cent. of this salt, the rest of its osmotic tension being due to other dissolved substances. If the membrane were absolutely "semi-permeable," water would pass from A to B until the two fluids were isotonic, *i.e.*, until A contained 1 per cent. Na Cl (we may regard volume of B as infinitely great to simplify the argument). If, however, the membrane permitted passage of salt, the course of events might be as follows: At first water would pass out of A, and salt would diffuse in until the percentage of Na Cl in A was equal to that in B. There would now be an equal partial pressure of Na Cl on the two sides of the membrane, but the total osmotic pressure of B would still be higher than A. Water would therefore still continue to pass from A to B more rapidly than the other ingredients of B could pass into A. As soon, however, as more water passed only from A, the percentage of Na Cl in A would be raised above that in B. The extent to which this occurs will depend on the impermeability of the membrane. As soon, however, as the Na Cl in A reaches a certain concentration it will pass over into B, and this will go on until equilibrium is established between A and B. Extending this argument to the conditions obtaining in the living body, we may conclude that neither the raising of the percentage of a salt in any fluid above that of the same salt in the plasma, nor the passage of a salt from a hypotonic fluid into the blood plasma, can afford in itself any proof of an active intervention of cells in the process.

Thus in the case of the pleura we seem to have a membrane which is very imperfectly semi-permeable. It is permeable to salts, but presents rather more resistance to their passage than to the passage of water. Hence on injecting ·5 per cent. Na Cl solution into the pleural cavity water passes from the pleural fluid into the blood, until the percentage of sodium chloride in the fluid is raised perceptibly above that in the blood plasma. The limit of the resistance of the pleural membrane to the passage of salt is, however, soon reached, and then salt passes from pleural fluid into blood; but in every case this passage is from a region of higher to a region of lower partial pressure. Hence at a certain stage of the experiment we find a higher percentage of salt in the pleura than in the blood-vessels, although the total amount of salt in the pleural fluid is less than that originally put in, or, in other words, salt has been absorbed.

We have already seen that the *effective* osmotic pressure of a substance, *i.e.*, its power of attracting water across a membrane, varies inversely as its diffusibility, or as the permeability of the membrane to it. What then will be the effect supposing that on one side of the membrane we place some substance in solution to which the membrane is impermeable?

We will suppose that A and B both contain 1 per cent. Na Cl, but that B contains in addition some substance x to which the membrane is impermeable. Since the osmotic pressure of B is higher, by the partial pressure of x, than that of A, fluid will pass from A to B by osmosis. But the consequence of this passage of water will be to concentrate the Na Cl in A, so that the partial pressure of this salt in A is greater than in B. Na Cl will therefore diffuse from A to B with the result that the former difference of total osmotic pressure will be re-established. Hence there will be a continual passage of both water and salt from A to B, until B has absorbed the whole of A. This result will be only delayed if the osmotic pressure of A is at first higher than B, in consequence of a greater concentration of Na Cl in A. There may be at first a flow of fluid

from B to A, but as soon as the Na Cl concentration on the two sides has become the same by diffusion the power of x to attract water from the other side will make itself felt, and this attraction will be proportional to the osmotic pressure of x.

We have an example of such a process in the absorption of salt solutions from the connective tissues by the blood-vessels, as well as in the absorption of the normal tissue lymph. The capillaries of the connective tissues of the limbs and peripheral parts of the body are almost impermeable to proteids. In consequence of this impermeability the fluid which is transuded from the capillaries under pressure contains very little proteid, whereas it contains exactly the same proportion of salts as does the blood plasma. It seems probable therefore that the proteid left in solution in the capillaries must exert a certain osmotic attraction on the salt solution outside the capillaries. It is easy to measure this attractive force. If blood serum be placed in a small thistle funnel, on the open end of which is stretched a layer of membrane soaked in gelatine, and the inverted funnel be immersed into salt solution which is isotonic or even hypertonic as compared with the serum, measured by the freezing-point, within the next two to four days fluid will pass into the funnel and rise up in its capillary stem to a considerable height. I have found that the osmotic pressure of the non-diffusible constituents of blood serum measured in this way amounts to between 30 mm. and 40 mm. Hg. Now although this osmotic pressure is so small, it is of an order of magnitude comparable with that of the hydrostatic pressure in the capillaries. This fact is of importance in that, whereas the capillary pressure determines transudation from the vessels, the effective osmotic pressure of the serum (proteids?) determines absorption by the blood-vessels. Moreover the osmotic attraction of the serum for the extravascular fluid will be proportional to the force expended in the production of this extravascular fluid, so that at any given time there must be a balance between the hydrostatic pressure in the capillaries and the production or absorption of fluid from the extravascular

spaces—a balance which is known to obtain under physiological conditions. If we increase the volume of circulating fluid we increase intracapillary pressure and the blood volume tends to diminish in consequence of increased transudation. If we diminish the capillary pressure by bleeding the animal, absorption will predominate over exudation, and the volume of circulating fluid will tend to increase towards its normal amount.

From this cursory study of some of the simplest examples of transference of fluids and salts across membranes, we may draw certain conclusions as to the main factors which are of importance for the process.

These are : (1) The permeability of the membrane to the dissolved substances. This permeability may be of the same character as the permeability of water, in which case the rates of passage of the dissolved substances across the membrane vary as their diffusibilities, and are therefore probably some function of their molecular weights. On the other hand the membrane may exhibit a certain attraction for, or power of dissolving, some dissolved substances to the exclusion of others, in which case there will be no relation between the diffusibilities and rates of passage of the dissolved substances.

(2) The osmotic pressure of the solutions. It is evident that the rules deduced by Heidenhain from the accepted theory of osmotic pressures, and quoted at the beginning of this article, are fallacious in consequence of a too narrow consideration of this second factor to the exclusion of the first. At the same time it must be confessed that our knowledge of the permeability of different membranes to different substances, as well as of the factors on which this permeability depends, is still in an embryonic condition. There can be no doubt that a careful exploration of this field of research would yield results not only interesting to the physicist, but also of incalculable value to the physiologist in his investigation of the phenomena of living things.

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